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Feeding Relationship of Two Species of Epizoic Amphipods and the Gray Whale, *Eschrichtius robustus*

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A mutualistic relationship exists with the gray whale, *Eschrichtius robustus,* and two species of Whale-Lice (Amphipoda: Cyamidae) because of the feeding regime of the cyamids. *Cyamus scammoni* Dall, 1872 and *Cyamus ceti* (Linnaeus 1758) apparently feed on the irritated epidermis of the gray whale surrounding the embedded, species-specific, ectocommensal barnacle *Cryptolepas rhachianecti* Dall, 1872 (Balanomorpha: Coronulidae). Feeding by the cyamids on the supporting skin may undermine the barnacle and ultimately cause it to become detached. The feeding area under and adjacent to the barnacle undergoes a color change from the original gray-black to white resulting in the white, circular scars characteristic to the gray whale. A third species of Cyamid, *Cyamus kessleri* Brandt, 1872 also occurs on the gray whale, but its role has yet to be determined.

The ecological relationship between whales and their external associates has been a source of conjecture at least from the time whale lice were first described by Linnaeus (1758), Brandt (1872), and Dall (1872). The gray whale, *Eschrichtius robustus,* with its three species of whale lice (*Cyamus scammoni, C. ceti* and *C. kessleri*), and one species of barnacle (*Cryptolepas rhachianecti*) is no exception. Leung (1976), in reference to the gray whale and its cyamid assemblage, speculated that "whale-lice are omnivorous, feeding on algal filaments and the outermost layer of skin tissue of the host" and possibly feeding as well on "the cutaneous tissue of the host, as the young customarily encases itself by piercing the delicate skin tissue or embedding itself in the cleavages of the sessile cirriped when it begins to maintain its livelihood." Noble and Noble (1976) characterized the whale-lice as "semiparasites" that burrowed into the skin of their host.

Methods

Data were obtained from seven beached gray whales (Table 1) and from observation of live, free-ranging gray whales. Live cyamid and barnacle assemblages were maintained, observed, and photographed *in situ* on stranded animals (Table 1). Live specimens of cyamid and barnacle associations, together with relatively fresh and undamaged sections of whale skin, were collected for further study (Figs. 1 and 5). All seven whales in Table 1 were collected from Southern California beaches during a six year period (1974–1979). None of the beached whales had been dead for more than two days. Observations and photographs were also made from various sized vessels and at close quarters (Fig. 3) ranging in the North from

Table 1. Strandings of Gray Whale in Southern California, 1974–1979.

Date collected/ observed	Sex	Estimated maturity[1]	Field number[2]	Total length	Stranding location
13 May 1974	Female	1 year	LACM-54544	6.9 m	San Clemente
20 Apr 1975	Female	20+ years	LACM-54545	13.0 m	Camp Pendelton
24 Feb 1976	Female	1 year	LACM-54548	7.9 m	Newport Beach
May 1976	Male	1 year	LACM-54549	7.7 m	Terminal Island
22 Nov 1976	Male	1 year	LACM-54550	6.5 m	Point Vincente
23 Jan 1977	Female	1–2 years	*WFS-1035	8.4 m	Los Angeles Harbor
20 Jan 1979	Male	1 year	*WFS-1042	7.2 m	Bolsa Chica State Beach

[1] After V. V. Zimushko 1970.

[2] Specimens and materials collected deposited in the Natural History Museum of Los Angeles County (LACM).

* No LACM numbers assigned; W.F.S. = W. F. Samaras Field Book Number (#4).

Point Conception, California, U.S.A. to Bahia Magdalena, Baja California Sur, Mexico in the south (including Scammon's Lagoon and Laguna Guerrero Negro in Baja California) from 1972 through 1981. Special attention was given to the distribution and density of cyamids and barnacles and to the types and shapes of scars and color patterns on the skin of gray whales.

Discussion

Cyamus scammoni (Fig. 2a) is the most easily identified of the three species (Fig. 2) of whale-louse found on the gray whale. It is the largest, most robust (20 mm in length), and darkest of the three. Live specimens are rather dull brownish-purple and are distinguished by two pairs of paired, corkscrew-like gills projecting ventrally from peraeon segments 3 and 4 (Margolis 1955; Hurley and Mohr 1957; Leung 1967).

A mature *C. ceti* (approximately 12 mm in length) is smaller than a mature *C. scammoni. C. ceti* is distinguished by its muted ochre color and two pairs of club-like gills. Each pair, emerging from peraeon segments 3 and 4, are carried laterally and curve anteriorly towards the cephalon (Fig. 2b). Segments 3 and 4 also carry one pair of short accessory gills projecting ventrally from the insertion of the primary gills. *C. kessleri* (c. 15 mm in length) resembles *C. ceti* but its peraeon is more laterally compressed and orange to coral in color. The long, baton-like gills, each pair emerging from peraeon segments 3 and 4, are also held latero-anteriorly but extend parallel to and beyond the cephalon (Fig. 2c). It has, like *C. ceti,* paired, bifurcated accessory gills on segments 3 and 4 which are attached ventrally at the insertion of the primary gills. These are short organs of subequal length.

There appears to be a species-oriented pattern of distribution of the cyamids on the gray whale as described by Rice and Wolman (1971) and Leung (1976). *C. scammoni* predominates in areas of heavy concentrations of barnacles on the head and trunk, particularly in wounds where necrotic tissue is present. *C. ceti* usually occurs anterior to the axilla of the pectoral fin and displays a distinct preference for skin folds, especially about the eyes, blowholes, throat grooves, and the gape of the mouth. *C. ceti* is a minor feeding competitor of *C. scammoni*

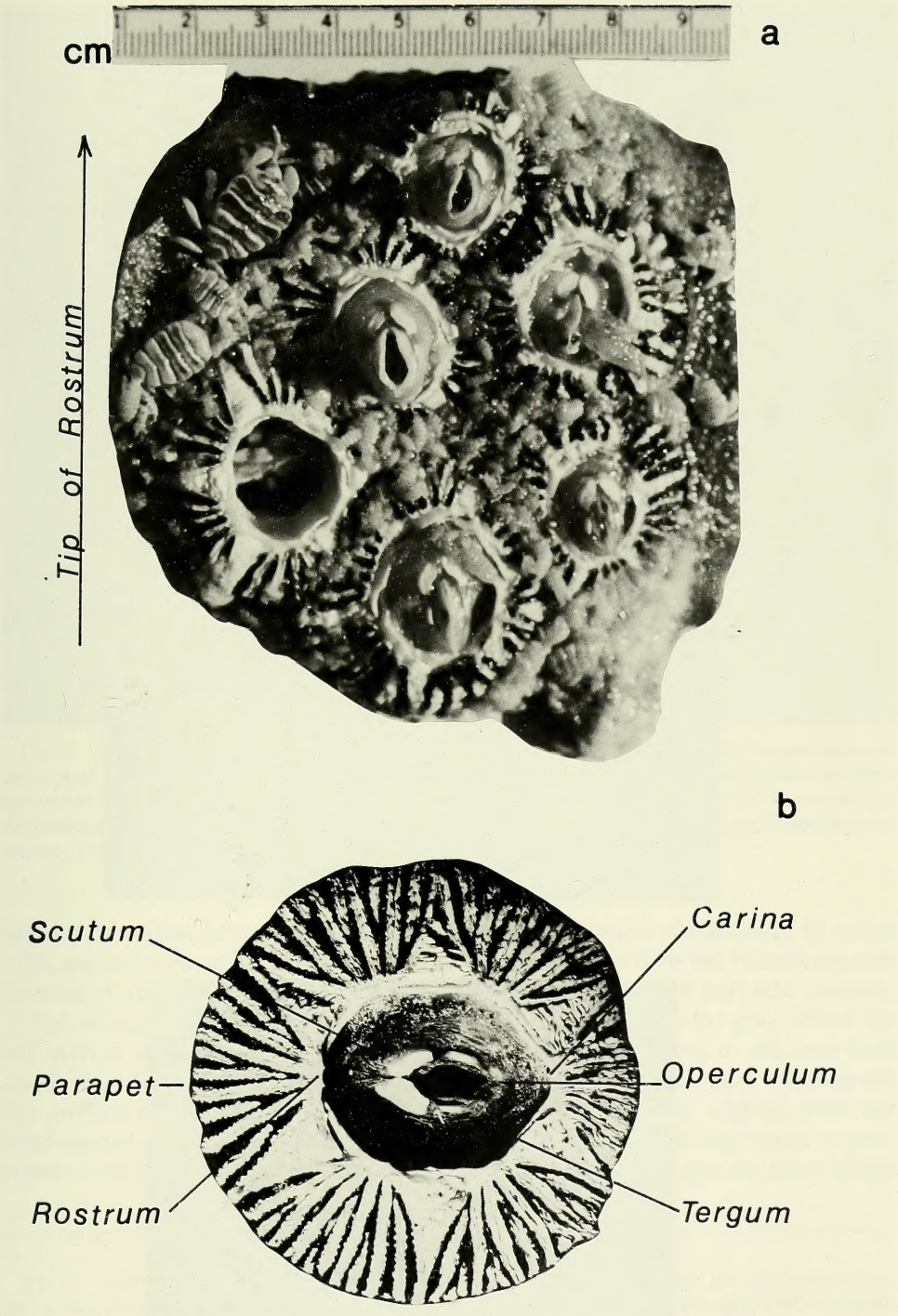
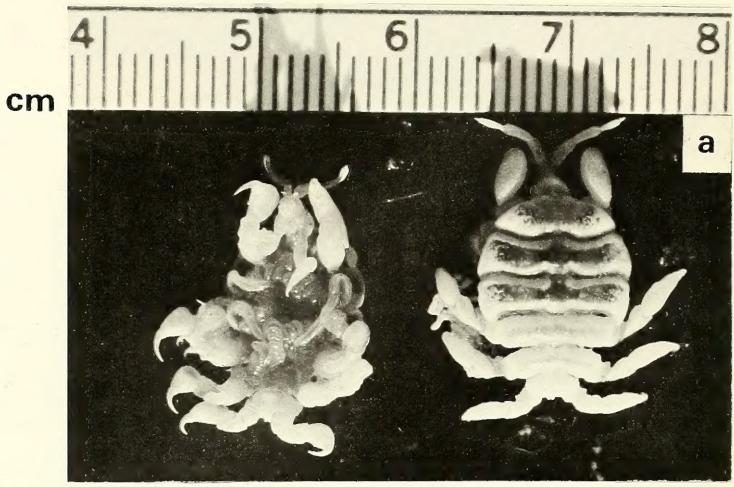
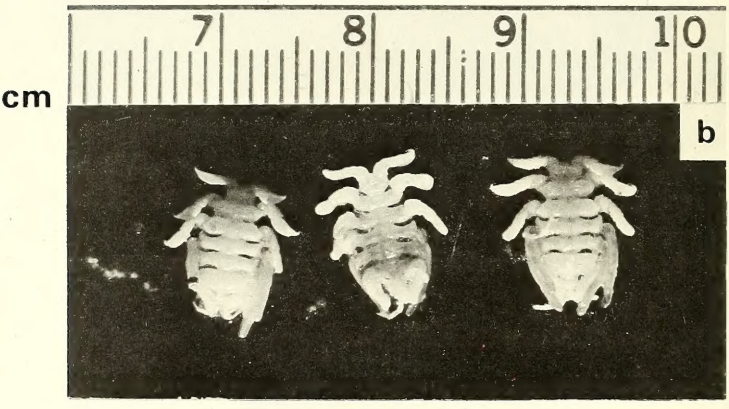


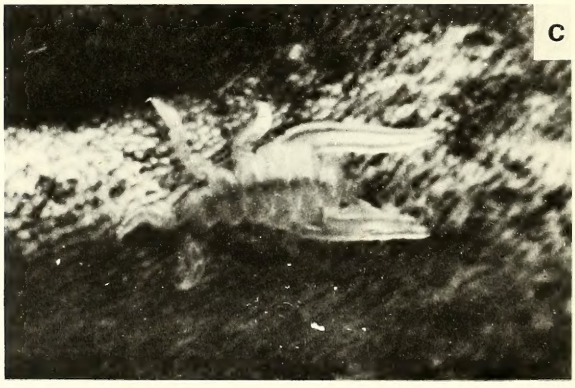
Fig. 1. a: A cluster of mature barnacles, *Cryptolepas rhachianecti,* from the rostrum of a gray whale (Table 1, WFS-1035). The apices of the scutae point in the general direction of maximum water-flow over the barnacle. The cirri of the barnacle in the upper right are extended through the open operculum. The identifiable cyamids are *Cyamus scammoni.* b: *Cryptolepas rhachianecti,* showing major anatomical features.



Cyamus scammoni



Cyamus ceti



Cyamus kessleri

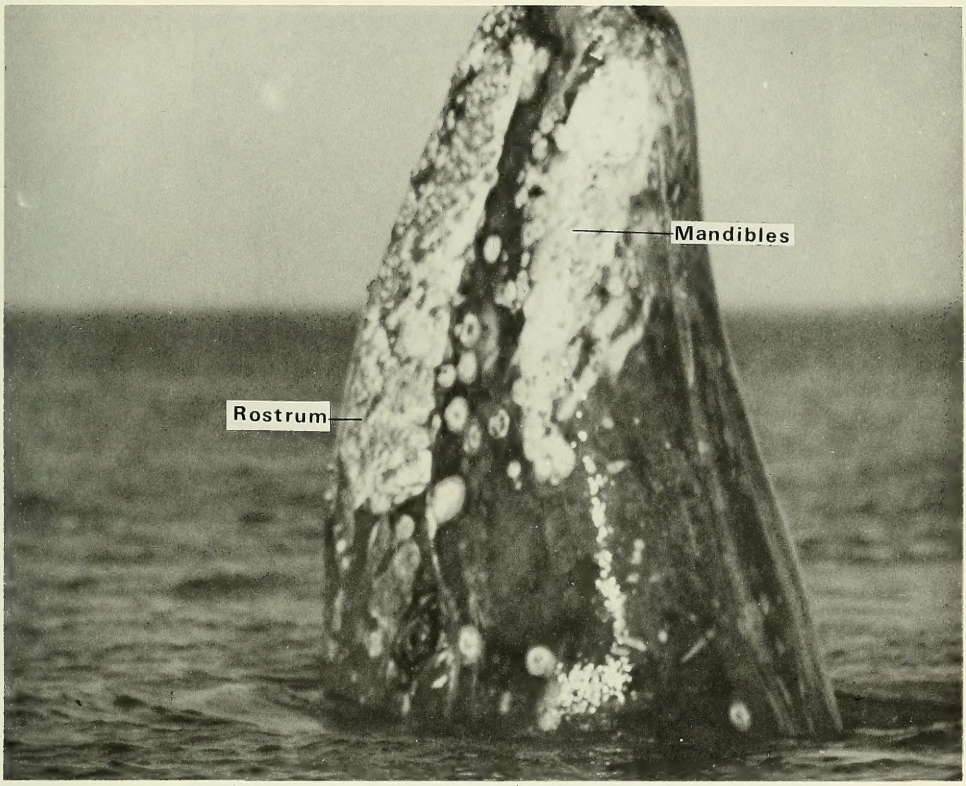


Fig. 3. Head of a spyhopping gray whale, showing areas of cyamid and barnacle concentration. In the area of the rostrum, the barnacles with their concomitant array of cyamids are packed together, forming an almost continuous mantle from the blowholes to the tip of the rostrum. On the mandibles, the barnacles are unevenly scattered either as isolated individuals or as small clusters. Photograph by Stephen Leatherwood (Scammon's Lagoon, Baja California Sur, Mexico).

around barnacles larger than 20 mm. *C. kessleri* is found consistently in trunk folds and orifices posterior to the pectoral fins, particularly in the mammary and urogenital openings. It has not been found in association with barnacle clusters.

The barnacle *Cryptolepus rhachianecti* is species-specific to the gray whale. Its orientation and alignment on the host may be directly related to efficient food acquisition (Rice and Wolman 1971). The rostrocarinal axes of the barnacle on the surface of the gray whales (Fig. 1) are characteristically aligned with the longitudinal axis of the whale (Rice and Wolman 1971). This alignment is consistent with the pattern of maximum laminar waterflow over specific parts of the

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Fig. 2. The three species of whale-lice (Arthropoda: Cyamidae) that infest the epidermis of the gray whale. a: *Cyamus scammoni,* the largest and numerically most abundant of the gray whale cyamids (Durham, unpublished). b: *C. ceti* is more commonly found anterior of the blowholes and in and around skin folds. c: *C. kessleri,* the least abundant of the three species of cyamids, is found primarily in the region of the urogenital aperture and anus (Samaras and Durham, pers. obs.).

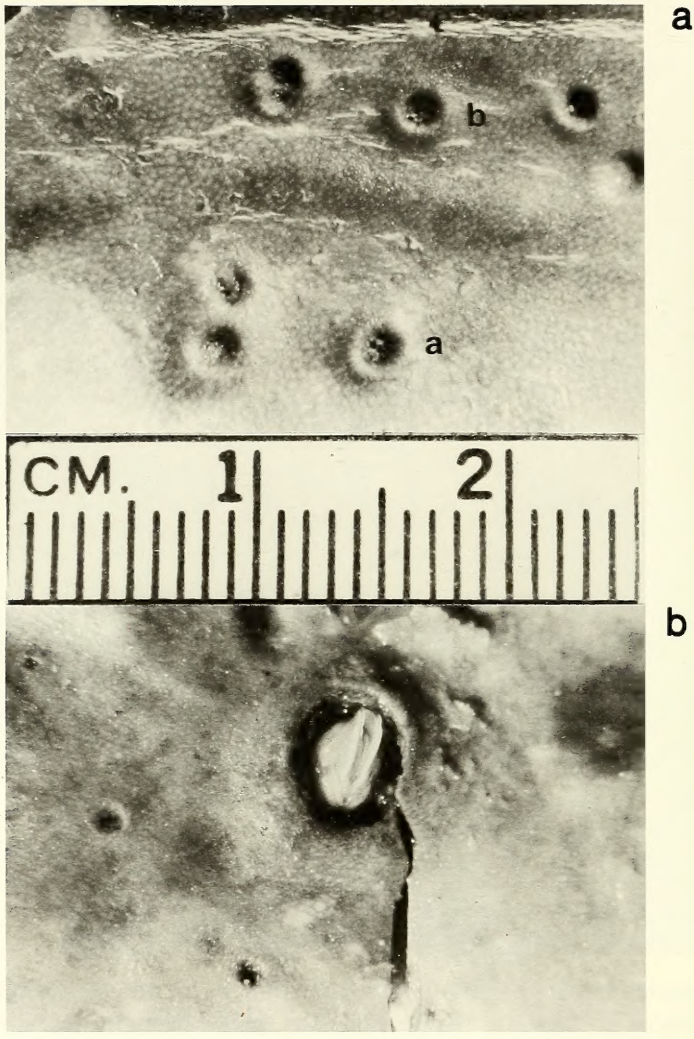

Fig. 4. Possible penetration and/or insertion pits. a: Miniscule, crater-like, attenuated pits in the epidermis of a yearling gray whale (Table 1, LACM-54548), apparently caused by the penetration or insertion mechanism of the cirriped cypris larvae. b: "Seed barnacle" that has not yet developed its protective, calcareous parapet. Notice that the surrounding crater and rim in the whales's epidermis are identical to those in *a* above. Magnification 4×; *a* and *b* to the same scale.

body, i.e., the rostrum and pectoral fins (Figs. 1a and 8) as described by Briggs and Morejohn (1972). With this orientation, the apices of the scutae, as well as the extended cirri of the barnacle, point in the direction of the whale's movement. Tightly packed clusters of barnacles in all stages of maturation, along with encrusting cyamids, may occur from the tip of the rostrum to the blowholes, forming an almost continuous mantle. A few small clusters are unevenly distributed over the throat region and jaws (Fig. 3). Barnacles are sporadically distributed from the blowholes posteriorly to the tips of the flukes. Large, mature barnacles may occur singly and occasionally with one or two small adjacent ones. Barnacles on

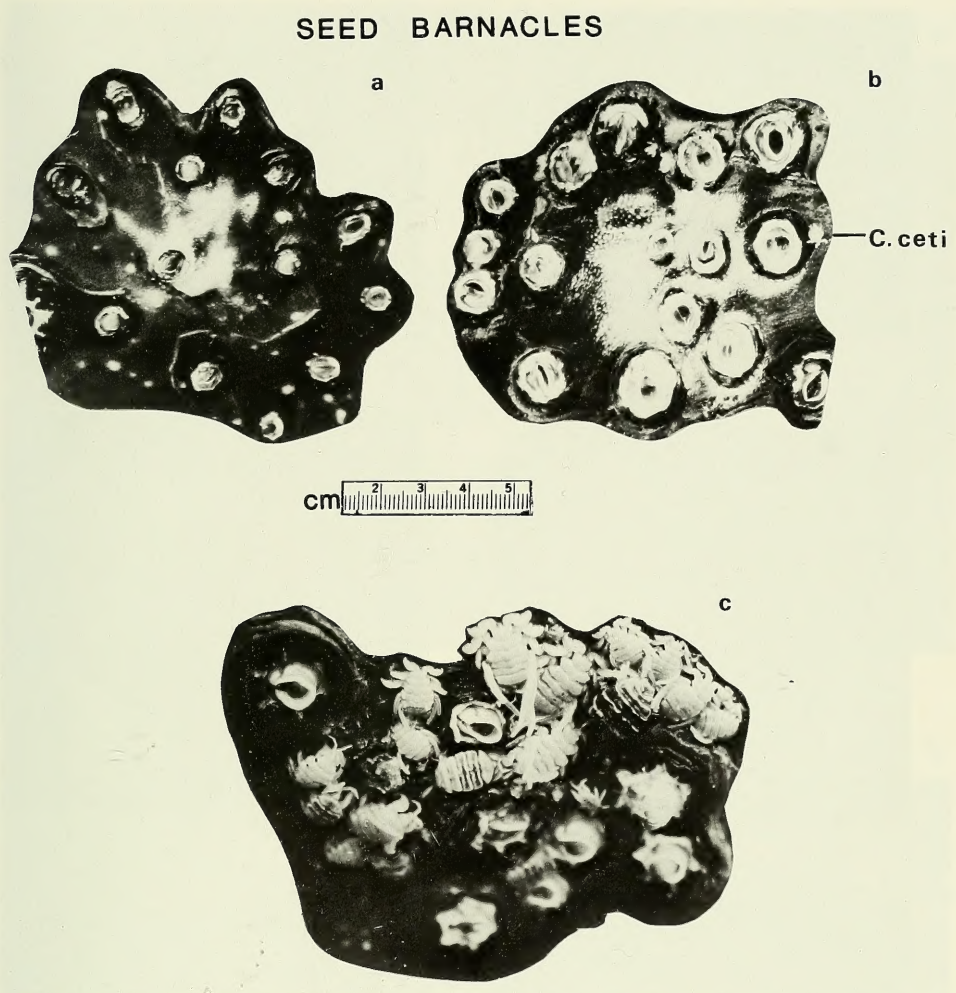

Fig. 5. a: Cluster of small seed-barnacles up to 5 mm in diameter. The white pigment transformation of dermis suggests that feeding by cyamids has commenced. b: Barnacles, 10–15 mm in diameter with calcareous parapets. The only large cyamid among these barnacles is *Cyamus ceti*. c: Feeding assemblage composed of at least eleven *C. ceti* and five *C. scammoni*. *a, b,* and *c* are the same scale. Photograph *c* by Terri Hoban (LACM-54544).

various parts of the gray whale may range in size from "seed" barnacles, 3–10 mm in diameter (Figs. 5a, b, 8, and 9), to mature ones, 40–60 mm in diameter (Fig. 6a).

The external anatomy of a mature barnacle is shown in Figure 1b. There are two major regions: one composed of six over-lapping plates forming the shell or parapet; and a second containing the opercular valves consisting of two scutae and two terga (Fig. 1b). The expanded and fluted basal portion of each of the six plates form the basis, and the primary attachment region of most cirripeds. In its dorsal aspect, the barnacle resembles a six-pointed star with a circle in its center. It is elliptical in cross-section.

As in most cirripeds, the free-swimming cypris larva is the stage during which

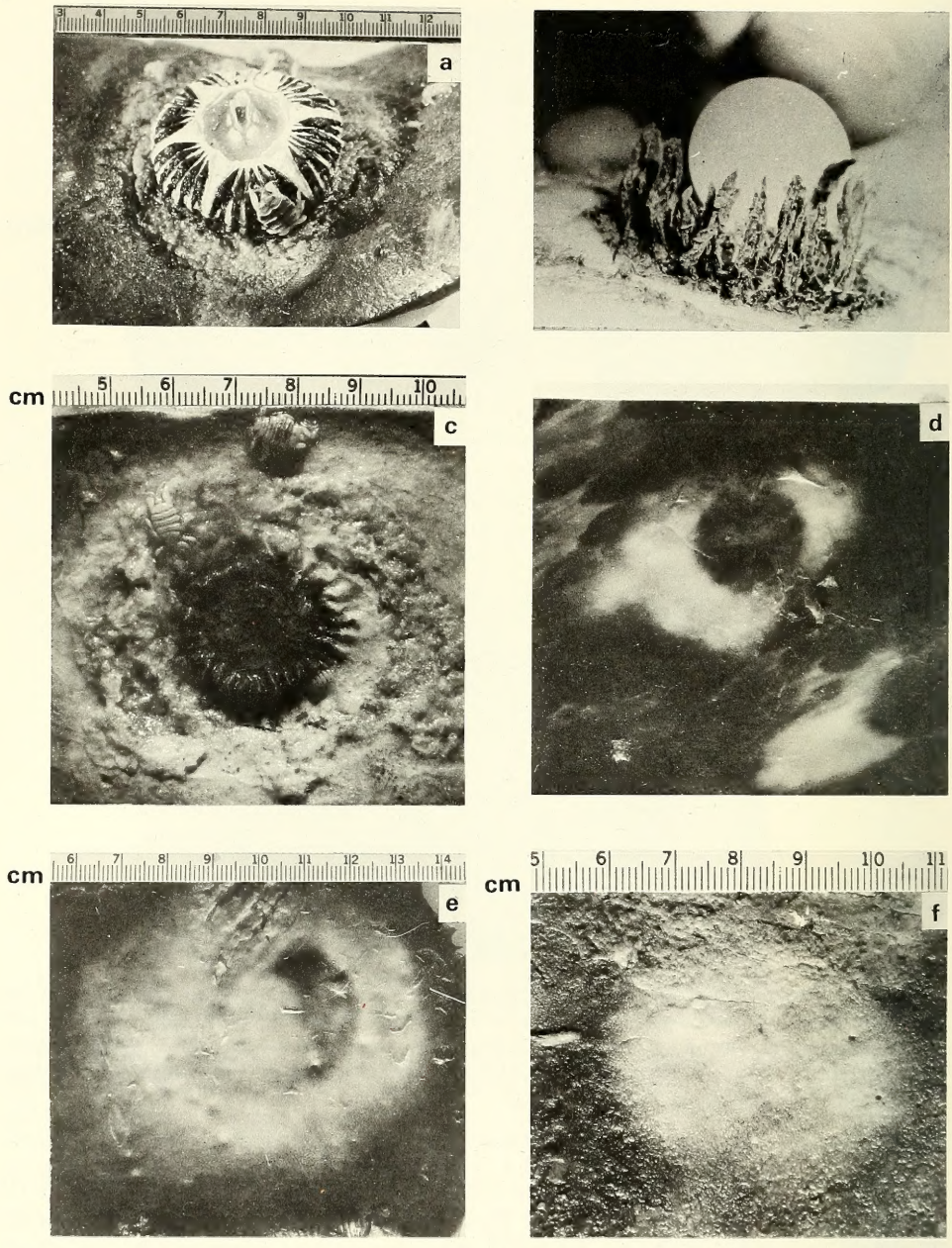

Fig. 6. Stages of scarification from terminal undercutting of *Cryptolepas rhachianecti* to complete dermal pigment transformation. a: A nearly completely undercut barnacle. The furrow excavated by feeding *Cyamus scammoni* is evident around its periphery. Basal excavation is also apparent. b: Site of a very recently removed barnacle. The fasicles of corium papillae that had grown between the barnacle's radial parapet flutes are apparent here as vertical structures. The object in the background is a penny. c: Characteristic scar created by peripheral basis-attachment processes. Cyamid induced excavation of the skin and subsequent pigment transformation are evident in this plate. The cyamids are *C. scammoni*. d: Wound left by the ablated barnacle. Cyamid-induced abrasion has almost completely healed with the replacement of the coreum, but pigment transformation from gray-black to white continues. e: Pigment transformation is almost complete. f: Complete pigment transformation has produced the characteristic round to oval barnacle scar seen on gray whales.

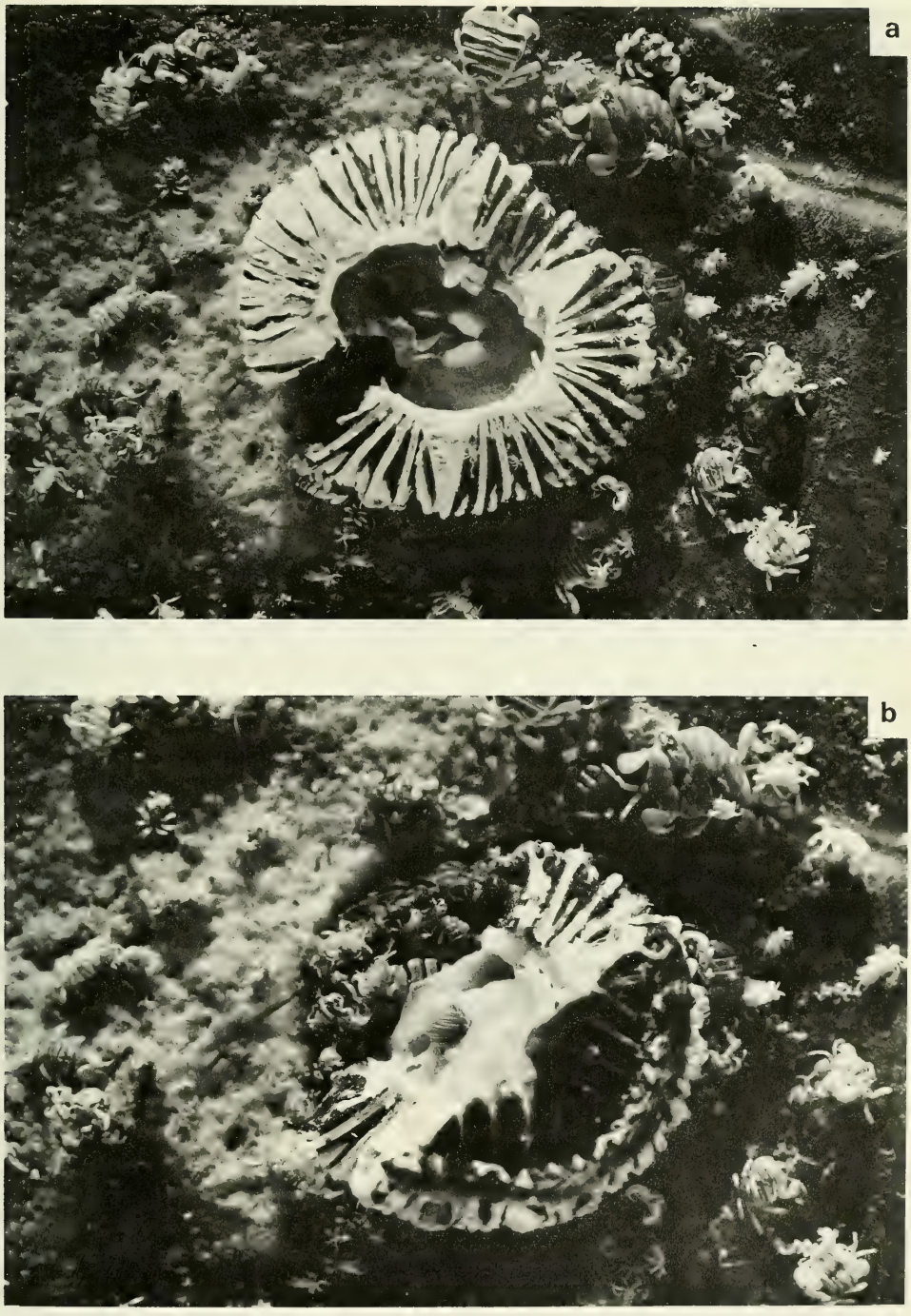

Fig. 7. Near terminally undercut, fully matured, *Cryptolepas rhachianecti.* a: Parapet was broken by authors. Notice cyamid-induced abrasions around periphery of barnacles. b: Parapet pulled back, revealing cyamids that had burrowed beneath the barnacle. This process ultimately relieves the supporting skin and the barnacle drops off the whale.

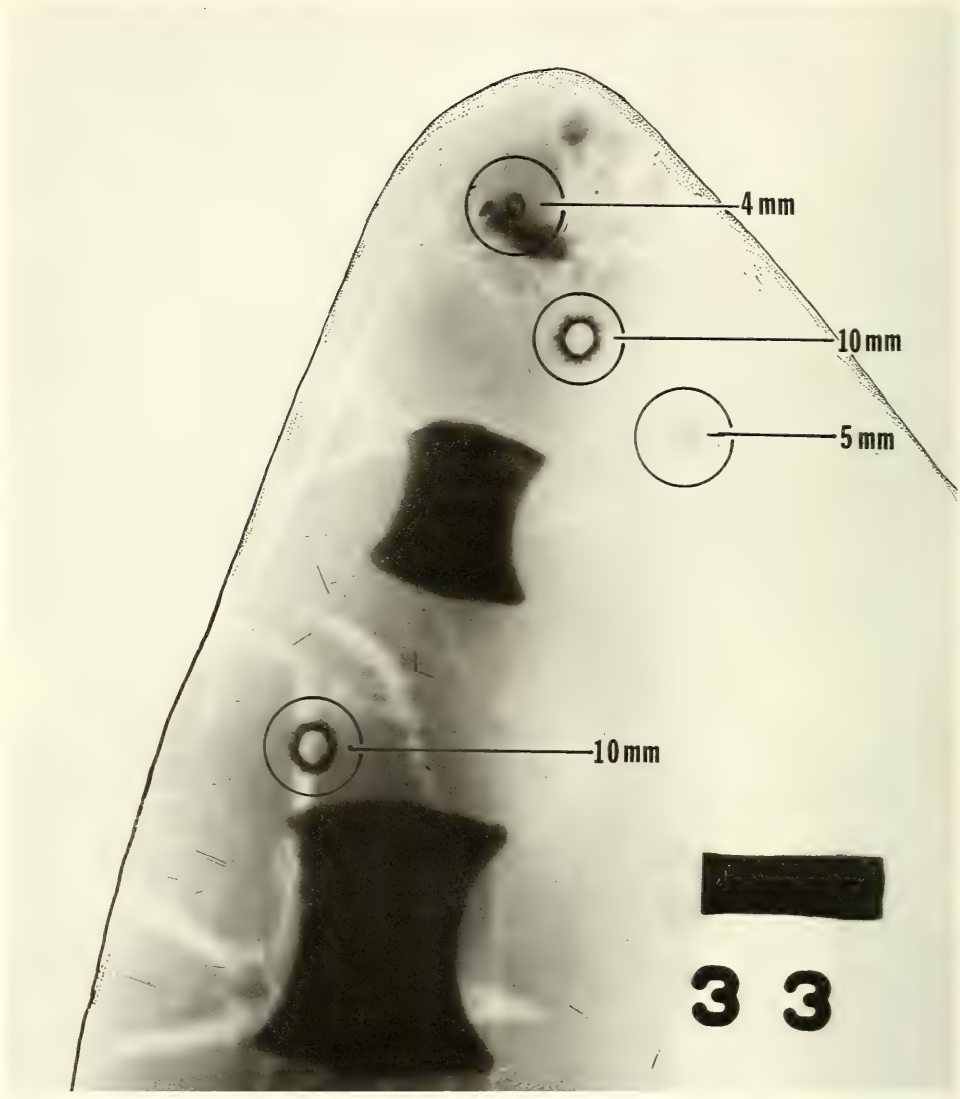

Fig. 8. X-ray of four seed barnacles on the distal tip of the right pectoral fin of a yearling, male gray whale (Table 1, LACM-54549).

attachment occurs. Initial attachment of the cypris larva of *Cryptolepas rhachianecti* has not yet been observed. Evidence based on the development and growth pattern of *C. rhachianecti,* along with the analysis of specimens by means of cross-sections and x-rays (Figs. 5a, b, and 9) of "seed" barnacle-rich gray whale skin, show that juvenile barnacles (3–10 mm in diameter) grow subcutaneously outward towards the epidermis. The juvenile barnacle (3–4 mm in diameter) appears to grow first vertically through the corium and corneum (Fig. 9b), then laterally through the epidermis (Figs. 1a, 5a, b and 7a). The presence of puncture-like pits or wounds in the immediate proximity of newly erupted "seed" barnacles (Fig. 4b) suggests possible similarities of initial attachment to that of parasitic cirripeds

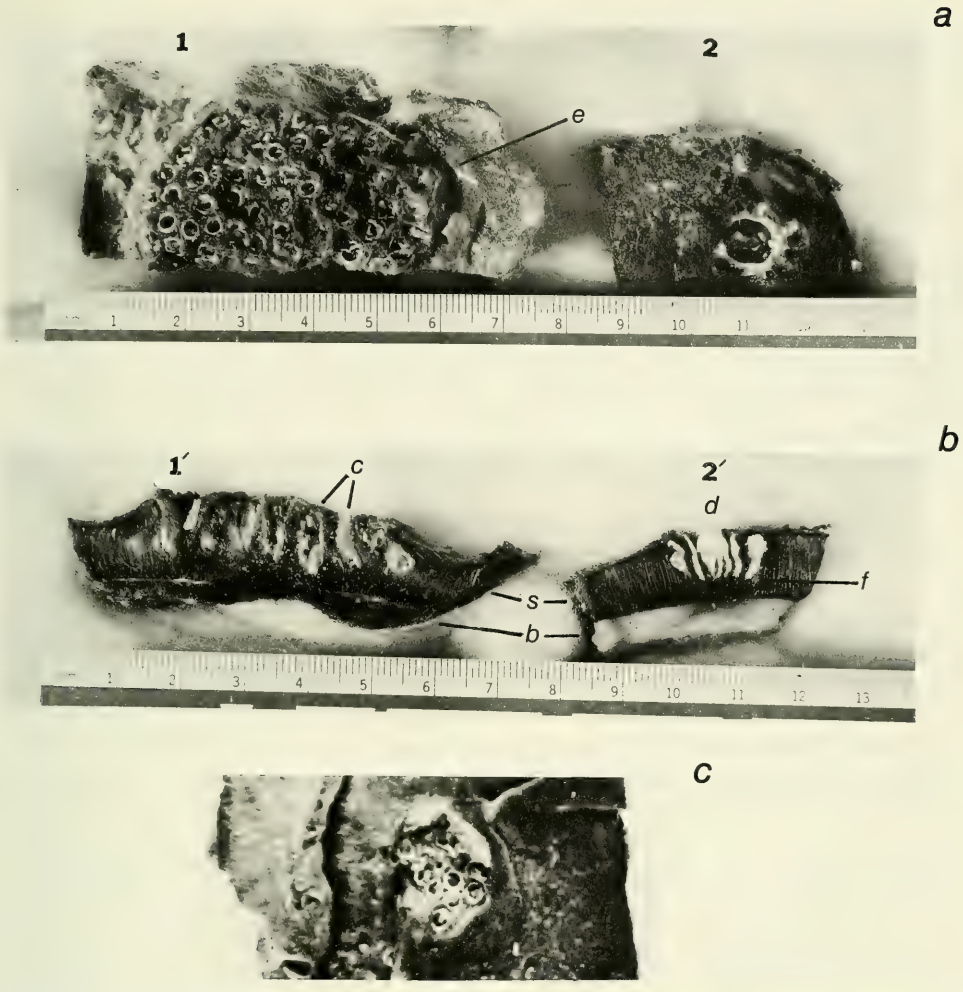

Fig. 9. a1: Dorsal view of a cluster of "seed" barnacles (*Cryptolepas rhachianecti*). Note surrounding ring of irritated, cornified dermis at e. a2: 17 mm in diameter barnacle. b1: Cross-sectional view of barnacle cluster a1 (dorsal is up). c: Note the cylindrical form and depth of penetration of the neoparapets (3–4 mm in diameter) as opposed to the fluted, elliptically-shaped, more mature barnacle at 2d; s is skin; b is blubber; f is the basis of the barnacle. c: The cluster c includes eighteen barnacles in an area about the size of a penny (15 mm in diameter).

of the genus *Sacculina* and other rhizocephalids. In *Sacculina* the cypris attaches by its antennae to a crab seta and inserts itself as a small mass of undifferentiated cells (see Green 1961; Barnes 1963) by means of a short dart-like tube that pierces the integument of the host. Figure 4a shows a series of attenuated pits of very small diameter in the skin of a young gray whale (Table 1 LACM-54548). These pits possibly mark the points of penetration and insertion of the cypris larvae of *C. rhachianecti.* In the immediate area of these pits is a small (3 mm in diameter) barnacle that has not yet fully developed its protective, calcareous parapet (Fig. 4b). Insertion of *C. rhachianecti* into the epidermis of the gray whale, therefore, might be similar to that of *Sacculina* into crabs.

The rate of growth of *C. rhachianecti* appears to be quite rapid from attachment to the fully mature cirriped (40–50 mm in diameter and about 20 mm thick). In February 1977 the senior author observed numerous gray whale calves, estimated to be six to eight weeks old, with a full array of large barnacles covering their rostra. They were leaving Laguna Guerrero Negro accompanied by their mothers and presumably starting their Northward migration to the Artic. Similar observations were made in Bahia Magdalena in mid-February of 1978.

Six of the whales in Table 1 were immature, their estimated ages varying from less than a year to two years. All six possessed complements of large, mature barnacles, as well as smaller ones in various stages of development. All of these animals bore white, circular barnacle scars characteristic of gray whales. It is believed, therefore, that the calf acquires its initial population of barnacles, via the free-swimming cypris larva stage, very soon after birth by direct contact with the mother and her concomitant population of barnacles and/or from planktonic *C. rhachianecti* cypris larvae in the surrounding waters in areas of high gray whale concentration such as Laguna Ojo de Liebre (Scammon's Lagoon) and Laguna San Ignatio. The rate of growth of the barnacle from insertion to fully maturity would then appear to be from two to three months.

The developing barnacle produces a cyst-like area of irritation on the surrounding skin of the whale. *Cyamus ceti* and *C. scammoni* appear to feed on the disturbed epidermis around and ultimately beneath the mature barnacle (Fig. 7b). Irritation or trauma of the host's tissue and a propensity for aggregation may attract the cyamids to feed in areas with barnacles. *C. scammoni* and/or *C. ceti* are always found clustered around barnacles on the gray whale. The whale's skin changes color from gray-black to white as feeding takes place. This also seems to be the case as surface wounds heal. Feeding progresses around and under the barnacle until it is completely undercut (Fig. 7). *C. ceti* appears to be the initial cyamid to begin feeding on the skin around juvenile barnacles. *C. ceti* has been observed feeding almost exclusively around barnacles up to 10 mm in diameter (Fig. 5c). *C. ceti* is rarely encountered in close proximity to barnacles larger than 20–30 mm in diameter. It is presumed that the larger, perhaps more aggressive, *C. scammoni* has supplanted it as the primary feeder. By the time the barnacle reaches 20–30 mm in diameter, the feeding cyamids have removed that portion of skin which initially overlapped the dorsal portion of the barnacle as far as the operculum. From this point on, the principal feeding area is around the immediate periphery of the barnacle (Fig. 6a). Both sexes and all stages of development of *C. scammoni* are found in this area (Fig. 1a).

Figures 6b and c show the sites of two recently undercut and detached barnacles. Figure 6b shows remnant supporting skin (corium papillae) between the flutes of the barnacle's parapet; and in Fig. 6c can be seen the impression left by the ventral surface of the parapet. Following extensive undercutting by feeding cyamids, final removal of the barnacle may be effected by: water currents along the skin of the whale; by the whale scraping along rocks or sand; and/or, by breaching.

On the stranded whales studied by the authors (Table 1), it appeared that at the site where a barnacle had recently been sloughed-off, the density of the cyamids decreased drastically. It is not known whether the cyamids move to the site of a new cirriped or simply end their life cycle. After the barnacle is detached, the black attachment site turns white in color and merges imperceptibly into the rest

of the feeding scar (Figs. 6d, e, and f). The final appearance of the feeding and attachment sites appears most commonly as a circular white scar (Fig. 6f) and less frequently as an oval scar (Fig. 6d).

The authors did not observe the direct transfer of cyamids from parent to a newborn gray whale calf. Indirect evidence indicates that contact, during and soon after birth, is the method by which the calf acquires its initial population of cyamids. Gray whale calves, estimated to be 3–4 weeks old, were observed by the senior author in Laguna Guerrero Negro and Bahia Magdalena with clusters of cyamids around their external nares and on the dorsum just posterior to the nares.

While diving around the caracass of an 8.4 m long female gray whale that had nearly been decapitated by a ship propeller (Table 1, WFS-1035), the same observer experienced an immediate transfer of hundreds of lice from the whale upon contact with areas of cyamid aggregations. Except for three large, mature *C. scammoni,* all the rest in this transfer were immature *C. scammoni* with possibly a few immature *C. ceti.* This probable transference of predominantly immature cyamids to the calf, coupled with the very rapid growth rate of the barnacle, should provide a ready food supply for them in a matter of days or, at the most, within two or three weeks.

This interaction between the cyamids and the barnacle represents an unique feeding arrangement. In feeding directly on the skin of the whale, *C. scammoni* and *C. ceti* could be referred to as parasites. On the other hand, cyamids feeding on damaged tissue in wounds and on irritated skin around erupting barnacles may aid in the healing process, as well as removing the barnacle, a source of irritation to the whale. This could be considered a mutualistic relationship. The barnacle is essentially a passive associate or "phoresitic commensual" (see Noble and Noble 1976).

After causing the removal of the barnacle, cyamids no longer continue to feed at the site. Consequently, the wound is allowed to heal with no visible evidence of the preexistence of the barnacle other than the change of color of the site from gray-black to white. The relationship seems to prove mutually beneficial to the cyamids and the whale, but not to the barnacle. Cyamids, at least *C. scammoni* and *C. ceti,* may provide a mechanism whereby the cirriped population is numerically controlled.

Limited data at hand indicate that *Cyamus kessleri* is an ectoparasite of the gray whale. Although the Cyamidae have been described as the only truly parasitic amphipods, *C. scammoni* and *C. ceti* may well be the exceptions.

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Of 310 collections totaling 4490 individuals of seven species of fleas from kit foxes in the Elk Hills area, southern San Joaquin Valley, California, 93.16% were the introduced *Echidnophaga gallinacea*; 5.1% *Cediopsylla inaequalis*; 1.25% *Pulex irritans*; 0.2% *Thrassis augustsoni*; 0.16% *Odontopsyllus dentatus*; 0.07% *Meringis californicus*; and 0.07% *Hoplopsyllus anomalus.* Circumstantial evidence based on the flea data suggest that lagomorphs make up most of the prey of *Vulpes macrotis mutica,* and that the desert cottontail may be more important than the black-tailed hare in the diet of this fox. The data also suggest that in Kern County the ratio of *Pulex* to *Echidnophaga* on kit foxes changes in favor of *Pulex* as the elevation increases.

In 1974 Congress directed the Secretary of the Navy, and subsequently the Secretary of the Department of Energy (DOE), to produce oil from Naval Petroleum Reserve No. 1 (NPR-1) at the maximum rate consistent with sound engineering practices (Public Law 94-258). NPR-1, or the Elk Hills Reserve, is located in western Kern County, California, at the southern end of the San Joaquin Valley about 30 miles west of Bakersfield. This part of the valley is true desert with an annual rainfall that averages less than six inches. The vegetation is Lower Sonoran grassland characterized by few or no trees, scattered shrubs, and an herbaceous ground cover of annual plants (Twisselman 1967). Since populations of an endangered subspecies of the kit fox, *Vulpes macrotis mutica* Merriam, (often called the San Joaquin kit fox) occurred on the site, DOE was obligated under the Endangered Species Act of 1973 (Public Law 93-205) to insure that measures taken to increase oil production did not jeopardize the continued existence of this fox.

The DOE initiated studies in 1979 to determine the ecology, distribution, and abundance of the kit fox on NPR-1, and to assess the possible impacts of various oil field activities on the subspecies and habitat critical for its survival. Among the goals of the program was to determine kit fox flea relationships that would aid in (1) establishing food habits based on the species and abundance of prey fleas collected from kit foxes, and (2) assessing the disease vector potential of *V. m. mutica* in areas frequented by large numbers of oil field workers. Only the first of these goals is considered in this paper.

What little has been published about kit fox fleas from the southwestern United States is based on a few scattered collections totaling less than 100 fleas, mostly from *V. m. arsipus* (Augustson 1943; Beck and Allred 1966; Nixon 1966; Turkowski 1974); and a statement by Morrell (1972) that "kit foxes [*V. m. mutica*] occasionally support large populations of fleas, identified as sticktight fleas,

Echionorhoya (sic) *gallinacea.*" The subspecies *arsipus* was later synonymized with *V. m. macrotis* by Waithman and Roest (1977).

Methods and Procedures

Kit foxes were livetrapped and then coaxed into cloth bags to facilitate handling, where they were weighed, measured, eartagged, fitted with radio transmitters, and examined. The head and neck were exposed so that a sample number of fleas could be collected. The number of fleas per sample depended somewhat on the degree of infestation and the amount of time available. No attempts were made to collect every flea seen, nor were other parts of the animals searched for fleas. Some foxes were captured more than once, but in this report each was regarded as a separate host. Sample collections were also obtained from carcasses of foxes found dead. Collection data included the date, sex and age of the host, plant associations, and elevation where the host was caught or found.

Fleas were collected from most common species of small mammals to determine host-flea relationships useful for evaluating food habits based on incidence of prey fleas on kit foxes.

Fleas were stored, processed, mounted for identification (when necessary), and labeled using standard methods. The distinctive sticktight fleas, *Echidnophaga gallinacea,* were determined and sexed using a 20× hand lens; most of them were returned to alcohol and not mounted. Otherwise, all fleas were permanently mounted on slides and currently (1984) are in my possession. Responsibility for all flea identifications is mine.

All males and some female *Pulex* from the Elk Hills and Mohave Desert collections and the Tooele County, Utah, kit fox projects mentioned in this report were carefully checked for the presence of *Pulex simulans* using illustrations in the literature (especially Hopla 1980) and specimens of *P. simulans* from coyotes in Oklahoma collected and determined by C. Hopla. No *P. simulans* were found. Not completely trusting my own judgement at the time, I also sent a series of the Utah material to the British Museum several years ago, where Frans Smit pronounced them correctly identified as *Pulex irritans* without question. The only published records of *P. simulans* from *V. macrotis* I know of are from Pima County, Arizona (Nixon 1966).

Results

The fleas collected from *V. m. mutica* are listed in Table 1 according to number, normal host and status of nonprey or prey species.

Nonprey fleas: The two kinds of fleas normally infesting kit foxes of Elk Hills and environs were the introduced sticktight flea, *Echidnophaga gallinacea,* and the so called human flea, *Pulex irritans,* the former being by far the most abundant. Of 310 collections totaling 4239 nonprey fleas from *V. m. mutica,* 98.7% were *E. gallinacea* and 1.3% were *P. irritans.* A sex ratio in favor of female *E. gallinacea* occurred throughout the year at Elk Hills but varied seasonally as follows: Winter (N = 1333) 1:1.9; Spring (N = 1587) 1:4.6; Summer (N = 929) 1:2.5; and Fall (N = 358) 1:4.7. The numbers reflect differences in number of foxes examined and not necessarily changes in seasonal abundance of sticktight fleas.

Prey fleas: The other five kinds of fleas from kit foxes at Elk Hills are ectoparasites of rabbits and rodents, mostly acquired through predation (Table 1). Over

Table 1. Fleas collected from *Vulpes macrotis mutica* at Elk Hills and environs listed according to species, normal hosts, and number.

Flea species	Number	Normal host(s) for area
Nonprey fleas:		
Echidnophaga gallinacea (Westwood 1875)	4183	kit fox
Pulex irritans Linnaeus 1758	56	carnivores
Prey fleas:		
Cediopsylla inaequalis ssp.	229	*Sylvilagus* and *Lepus*
Thrassis augustsoni Hubbard 1949	9	*Ammospermophilus nelsoni*
Odontopsyllus dentatus (Baker 1904)	7	*Sylvilagus* and *Lepus*
Meringis californicus Augustson 1953	3	*Dipodomys ingens* *Dipodomys nitratoides* *Dipodomys heermanni*
Hoplopsyllus anomalus (Baker 1904)	3	Sciurids
Total	4490	

90% of the 251 prey fleas recovered were *Cediopsylla inaequalis,* commonly found on cottontails but much less frequently on black-tailed hares, *Lepus californicus,* even where both are ecologically sympatric. In Monterey County, California, for example, Linsdale and Davis (1956) found that 52.1% of 841 fleas from *Sylvilagus audubonii* were *C. inaequalis,* while no fleas of this species were collected from *L. californicus,* although the sample size was smaller. Host preferences of the rarer lagomorph flea, *Odontopsyllus dentatus,* are less clear, but again *Sylvilagus* sp. appeared favored over *Lepus,* both in California (Linsdale and Davis 1956) and elsewhere (Holland 1949; Beck and Allred 1966). It should be pointed out that the denning and nesting habits of cotton tails make them more suitable as hosts for fleas than those of black-tailed hares, which seldom make or take refuge in burrows.

Only 6% of the prey fleas are normally hosted by rodents. These included nine *Thrassis augustsoni,* a rather host specific flea of the Nelson antelope ground squirrel, *Ammospermophilus nelsoni,* (Stark 1970), and three *Hoplopsyllus anomalus,* a somewhat less host specific flea that often parasitizes sciurids, especially *Spermophilus beecheyi* during summer months. The small number of the heteromyid flea, *Meringis californicus,* seemingly discounts the importance of *Dipodomys* in the diet of *V. m. mutica* sampled during this study, although kangaroo rats have been reported to be an important food item of this fox (Grinnell et al. 1937; Hawbecker 1943; Morrell 1972).

The two fleas, *Monopsyllus wagneri* and *Malaraeus telchinum,* commonly found on deer mice, *Peromyscus maniculatus,* and less frequently on western harvest mice, *Reithrodontomys megalotis* at Elk Hills were not collected from kit foxes there.

Discussion

How and when *E. gallinacea* became part of the flea fauna of Elk Hills and environs is conjectural. Elsewhere in the west, introductions of this economically important pest have been traced back to hen houses (Hubbard 1947; Linsdale and Davis 1956; and others), while Stewart (1932) thought birds that frequent

farmyards such as the English sparrow, Brewer's blackbird, and quail were potential dispersal agents of sticktight fleas from poultry to wild animals. Judging from its abundance on *V. m. mutica,* ecological factors and host associations must have been more favorable for the naturalization of *E. gallinacea* in the Elk Hills region than other places where kit fox fleas have been collected. Here at the lower elevations (av. 288.2 m), almost 99% of the nonprey fleas from *V. m. mutica* were sticktight fleas while less than 2% were *P. irritans.* Elsewhere in Kern County this ratio changed in favor of *Pulex* with local increases in altitude suggesting that the human flea is less well adapted than *E. gallinacea* to the hottest, driest parts of the area. For example, at Elkhorn Plain some 40 km southwest of Elk Hills, 17 collections totaling 124 nonprey fleas from *V. m. mutica* trapped at elevations averaging 701.5 m were 75% *E. gallinacea* and 25% *P. irritans.* In the Mohave Desert along the base of the Rand Mountains near California City about 135 km east of Elk Hills (av. elevation 696.6 m), 292 nonprey fleas from *V. m. macrotis* collected during another study (O'Farrell and Gilbertson, unpublished data) were 17% *E. gallinacea* and 83% *P. irritans.* Both of these fleas were also found on *V. macrotis* ssp. in Nye County, Nevada (elevation not given but known to be several hundred meters higher than Elk Hills), where the Mohave Desert contacts the Great Basin about 161 km northwest of Las Vegas (Beck and Allred 1966), and two counties of Arizona (Turkowski 1974). These collections were too small to calculate ratios but suggest that *P. irritans* was the most common flea on kit foxes in both areas. Evolved differential adjustments to climate probably account for changes in the ratio of *Echidnophaga* to *Pulex* at different altitudes in Kern County and elsewhere. In the desert valleys of Tooele County, Utah, where elevations averaged 1385 m, 567 nonprey fleas collected from *V. m. nevadensis* were all *P. irritans* including several found alive on a carcass after it lay frozen along a roadside for at least five days (Egoscue 1962 and unpublished data). This area is beyond the northern limits of *E. gallinacea* in Utah (Beck 1955; Stark 1958), where ground squirrels collected at the lower elevations in the southern part of the state were the most frequently recorded hosts. Despite the occurrence of suitable hosts throughout Utah, the sticktight flea has not spread as a feral species or as a pest on poultry beyond areas reported by Beck and Stark (R. S. Roberts, Extension Entomologist, Utah State University, personal communication 1983). The kit fox is not uncommon in southern Utah (McGrew 1977), but I know of no flea records from *V. macrotis* collected in the southern counties. Since *P. irritans* occurs as far north in Canada as Hudson Bay (Hopla 1980), it obviously withstands colder climates than the sticktight flea which has been reported to die at freezing temperatures in the laboratory (Hubbard 1947). Of greater significance to fleas would be favorable or unfavorable differences in microclimates of burrows associated with differences in macroclimates.

While prey fleas on predators or lack of them can provide clues about food habits, such evidence can be misleading. Prey species without host-specific fleas would go undetected. For example, the range of *Monopsyllus exilis,* the only true flea of *Onychomys,* does not include the San Joaquin Valley (Johnson 1961) making it impossible to identify the southern grasshopper mouse, *Onychomys torridus,* found there as a prey item based on flea samples from predators of the region. Small mammals may be swallowed whole so quickly after being caught that there is no opportunity for fleas to transfer from host to predator. Fleas may

manage to transfer from a host that is cached by the fox and never eaten. Nocturnal predators might acquire the fleas of diurnal hosts accidentally at night while investigating burrow entrances or from carrion. Many small mammals have very low flea indices which presumably lessens the chances of predators acquiring their fleas. Such indices were not determined for prey species at Elk Hills, but studies elsewhere are indictive. In Monterey County, California, Linsdale and Davis (1956) reported the mean annual number of fleas per infested host was 1.7 for deer mice, 1.1 for western harvest mice, 2.4 for a species of *Dipodomys* and 10.5 for the desert cottontail. Negative results were not recorded in that study, but in western Utah 20 to 33⅓% of 474 deer mice were without fleas (Egoscue 1976). Some species are also highly seasonal in numbers and may disappear entirely for months.

The evidence provided by prey fleas about the food habits of predators should be augmented and or corroberated, when possible, by scat analyses, examination of digestive tracts, and prey remains around dens.

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A Habitat Analysis of the Nearshore Marine Fishes from Southern California

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This study synthesized the results of 38 ichthyofaunal studies from a wide range of habitats within the Southern California Bight. Quantitative clustering of sites based on species composition yielded nine distinct groups designated as bay/estuary (BE), open coast sandy beach (OC), harbor/nearshore soft bottom (H/NSB), nearshore midwater (MW), offshore soft bottom (SB), rocky intertidal (IT), shallow rock reef (SRRF), deep rock reef (RRF), and kelp bed (KB). Clustering of the 105 species produced 19 groups of both widespread and habitat specific species. Calculation of H′ and J′ diversity indices yielded virtually indistinguishable rankings among habitat types with the SB, KB, and RRF habitats showing highest fish diversity in general and MW, BE, and IT the lowest. Possible explanations for the observed patterns of diversity among the nine major habitats are discussed.

The nearshore marine environment off Southern California hosts a diverse and transitional ichthyofauna containing both northern (Montereyan) and southern (San Diegan) fish species (Horn and Allen 1978). To a large extent, this high faunal diversity reflects the great variety of marine habitats that are available to nearshore fishes within the Southern California Bight (e.g., bays and estuaries, harbors, offshore soft bottom, rocky intertidal, kelp bed, and rocky reefs) (Horn 1980). The fishes of these various Southern California habitats have been the subject of numerous ichthyofaunal studies (see Table 1) over the past 25 years. This analysis represents the first attempt at a bight-wide synthesis of information on fish species and the habitats in which they occur.

Specifically, the main purposes of this paper are to: 1) present a quantitative classification of nearshore marine habitats in the Southern California Bight based on the affinities of their fish assemblages; 2) present a quantitative classification of fish species according to habitat affinity; 3) describe the general patterns of diversity within the various habitat types; and 4) attempt to explain the patterns of fish diversity within habitats.

Methods

Data on species composition and relative abundances of fishes from 38 ichthyofaunal studies (Table 1) were compiled for analysis. These studies ranged in latitude from Naples Reef (just northwest of Santa Barbara) to Imperial Beach (just south of San Diego) (Fig. 1). Most of the habitats studied were located within

Table 1. Study localities utilized in the present synthesis with locale designation, sampling methods, sample sizes, duration and source of information. (BS = beach seine; DC = diver census; DT = diver transect; GN = gill net; LP = lampara net; OT = otter trawl; P = poison (rotenone or quinaldine). Under OCCAR; Carpenteria (1) = OCCAR 1, Point Dume (2) = OCCAR 2, etc. on Figure 1. Diver transects include both diver counts along a tape and counts made using cinetransects. In diver censuses, counts were made over a time period, not along a transect.

Desig-nation	Locality	Sampling methods	Sam-ple size	Dura-tion of study (months)	Source
BEANHB	Upper Anaheim Bay	BS, GN, OT	?	24	Lane and Hill (1975)
BECOL	Colorado Lagoon	BS	34	12	Allen and Horn (1975)
BEML	Mugu Lagoon	BS	48	12	Quammen (unpubl. data)
BEOANH	Outer Anaheim Bay	BS, OT	88	12	Lane and Hill (1975)
BEUNB	Upper Newport Bay	BS, GN, OT	336	13	Horn and Allen (1981)
HCABCH	Cabrillo Beach	BS, GN, OT	216	12	Allen et al. (1983)
HLAST	Outer Los Angeles-Long Beach Harbor	OT	76	12	Stephens et al. (1974)
HLNB	Lower Newport Bay	BS, GN, OT	102	18	Allen (1976)
HSBSP	San Pedro Bay	OT	33	27	Stephens et al. (1973)
ITCOM	Corona del Mar	P	9	4	Cross (unpubl. data)
ITPR	Pin Rock, Catalina Island	P	3	9	Allen (unpubl. data)
ITPV	Palos Verdes Peninsula	P	30	132	Walker (unpubl. data)
KBNR	Naples Reef near Santa Barbara	DT	297	48	Ebeling et al. (1980)
KBQUST	Del Mar, BathTub Rock and Papalote Bay (Baja Calif.)	P	3	15	Quast (1968)
KBSC	Santa Cruz Island	DT	331	48	Ebeling et al. (1980)
KBSMK	San Mateo Kelp Bed	DT	310	4	DeMartini (unpubl. data)
KBSOK	San Onofre Kelp Bed	DT	660	4	DeMartini (unpubl. data)
MWLMPD	San Onofre-Oceanside (18–27 m depth)	LP	196	18	Allen and DeMartini (1983)
MWLMPM	San Onofre-Oceanside (12–16 m depth)	LP	176	18	Allen and DeMartini (1983)
MWLMPS	San Onofre-Oceanside (8–11 m depth)	LP	267	18	Allen and DeMartini (1983)
OCALSO	Aliso Canyon Beach	BS	50	9	Tetra Tech (1977)
OCCAR	Carpinteria (1), Point Dume (2), Redondo Beach (3), Belmont Shores (4), Laguna Beach (5), Coronado (6)	BS BS BS BS BS BS	451	44	Carlisle et al. (1960)
OCEMB	Enlisted Man's Beach	BS	15	8	Tetra Tech (1977)
OCSO	San Onofre Beach	BS	24	8	Tetra Tech (1977)
RRFHB	Hermosa Beach	DC	16	12	Turner et al. (1969)
RRFMAL	Malibu Beach	DC	13	12	Turner et al. (1969)
RRFSM	Santa Monica Beach	DC	14	12	Turner et al. (1969)
SBCAT	Catalina Island	OT	18	11	SCCWRP (unpubl. data) and Allen (unpubl. data)
SBHB	Huntington Beach	OT	192	12	Horn (unpubl. data)

Table 1. Continued.

Designation	Locality	Sampling methods	Sample size	Duration of study (months)	Source
SBNB	Newport Beach	OT	12	12	Allen (1976)
SBOC	Orange County Outfall	OT	116	108	SCCWRP (unpubl. data)
SBPV	Palos Verdes Peninsula	OT	238	72	SCCWRP (unpubl. data)
SBSM	Santa Monica Bay	OT	705	72	Carlisle (1969)
SBSO	San Onofre-Oceanside	OT	384	12	DeMartini and Allen (in press)
SRRFKH	King Harbor, Redondo Beach	DT	667	72	Stephens and Zerba (1981)
SRRFMB	Mission Bay Breakwater	DT	14	12	DeMartini and Roberts (1981)
SRRFPV	Palos Verdes Peninsula	DT	305	96	Stephens (unpubl. data)
SRRFSG	La Jolla–Pt. Loma	DT	16	6	DeMartini (1981)

4 km of the Southern California mainland; three studies occurred at Santa Catalina and Santa Cruz Islands (Fig. 1). Relative abundances of species in each study were expressed as the percentage that the species represented in the total number of individuals (juveniles and adults could not be distinguished). For a species to be included in the analysis it must have had a relative abundance of >0.1 percent in the study. The species abundances were, therefore, standardized to 100 percent in each study for subsequent numerical classification. This approach to quantifying species within habitats carried two major, but not unreasonable, assumptions. First, I assumed that the methods employed were those most effective for sampling fishes in that particular habitat. Second, the methods employed sampled the most abundant and common species in the habitat in proportion to their actual abundances. A synthesis like that presented here is wrought with problems which must be considered before formulating conclusions. These inherent problems (see Table 1) include: 1) the major habitats were physically different; 2) the methods employed differed between habitats; 3) the durations of the studies were variable; 4) sample sizes (unit of effort and total effort) were variable; 5) some studies employed multiple methods while others used only one method; 6) the expanse of each of the sampling areas was different; and 7) major habitats (e.g. kelp beds) were subject to regional variations in species composition. The first two problems (1 and 2 above) were addressed by the two major assumptions stated previously. The general importance of items 3–5 within habitat diversity was evaluated using correlation analysis. Expanse of sampling area was extremely difficult to determine for most studies and could not be evaluated directly. Lastly, the factor of regional variation figured prominently in the interpretation of species associations within major habitats.

Classifications of both species and habitats were accomplished by computer-aided cluster analysis using the Ecological Analysis Package (E.A.P.) written by Robert W. Smith. The Bray-Curtis Index of Dissimilarity (Clifford and Stephenson 1975) was calculated for square-root transformed species abundance data. Only those species having a minimum occurrence of 3 or a minimum summed per-

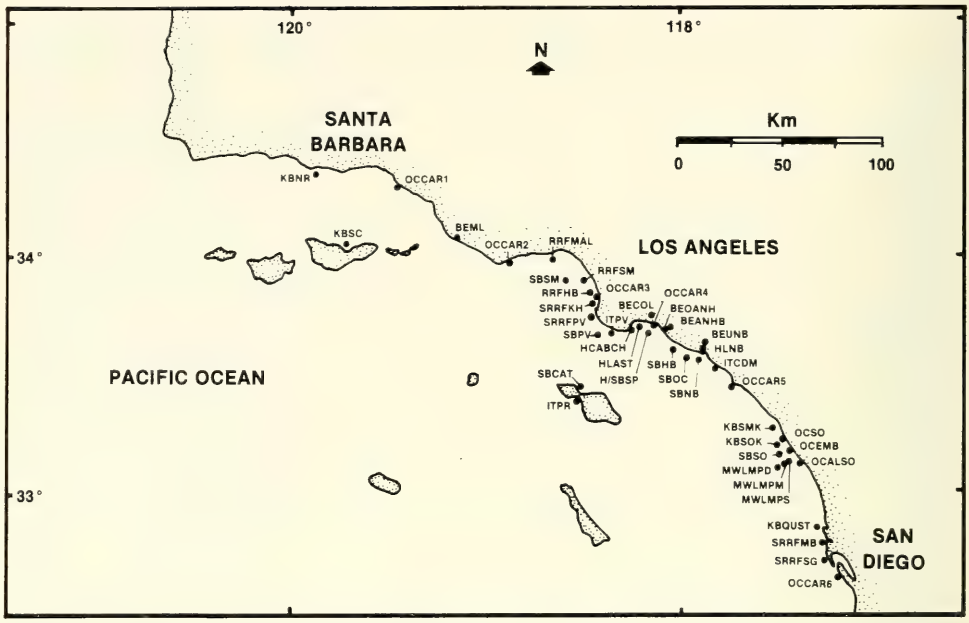

Fig. 1. Map of the Southern California Bight with the locations of the study sites (see Table 1 for locale designations).

centage of ≥ 5.0 were clustered. These minimum inclusion values resulted in a data matrix that included 105 species of fish within the 38 habitats. Flexible sorting was utilized to maximize separation between groups. It was necessary to exclude *Engraulis mordax* (northern anchovy) from the classification of habitats due to its overwhelming abundance in certain studies. The numerical dominance of *E. mordax* consistently led to habitat groups based solely on its presence regardless of other associate species.

Patterns of diversity within the habitat types defined by cluster analysis were examined in two ways. First, cumulative abundances of the ten most numerous species were plotted for each habitat. The resultant curves served to illustrate relative dominance and equitability within the ichthyofaunae of the various habitat types. Second, Shannon-Weiner (H′) information function (Shannon and Weaver 1949) and the evenness index (J′) of Pielou (1966) were calculated using all species with >0.1% abundance in each habitat. Only 35 of the habitat sites were used for calculations of diversity. Relative abundances had to be estimated for the BEANHB site. Only biomass measures were available for the KBQUST site. Samples at the SBCAT site were temporally erratic.

The number of species (S) making up >0.1% of the catch was found to depend heavily on duration of the study in three of the eight major habitats (IT, SRRF, and KB, see below) (Spearman rank correlations, r_s, $P < 0.1$). Additionally, within the remaining five habitats, the unmistakable trend was for studies with longer duration to have more species. The bias introduced by duration of the study on S was due to the addition of more, rare species over time. It was, therefore, necessary to de-emphasize S in the overall analysis. The H′ and J′ indices were not affected as adversely by duration of the study since rare species add very little

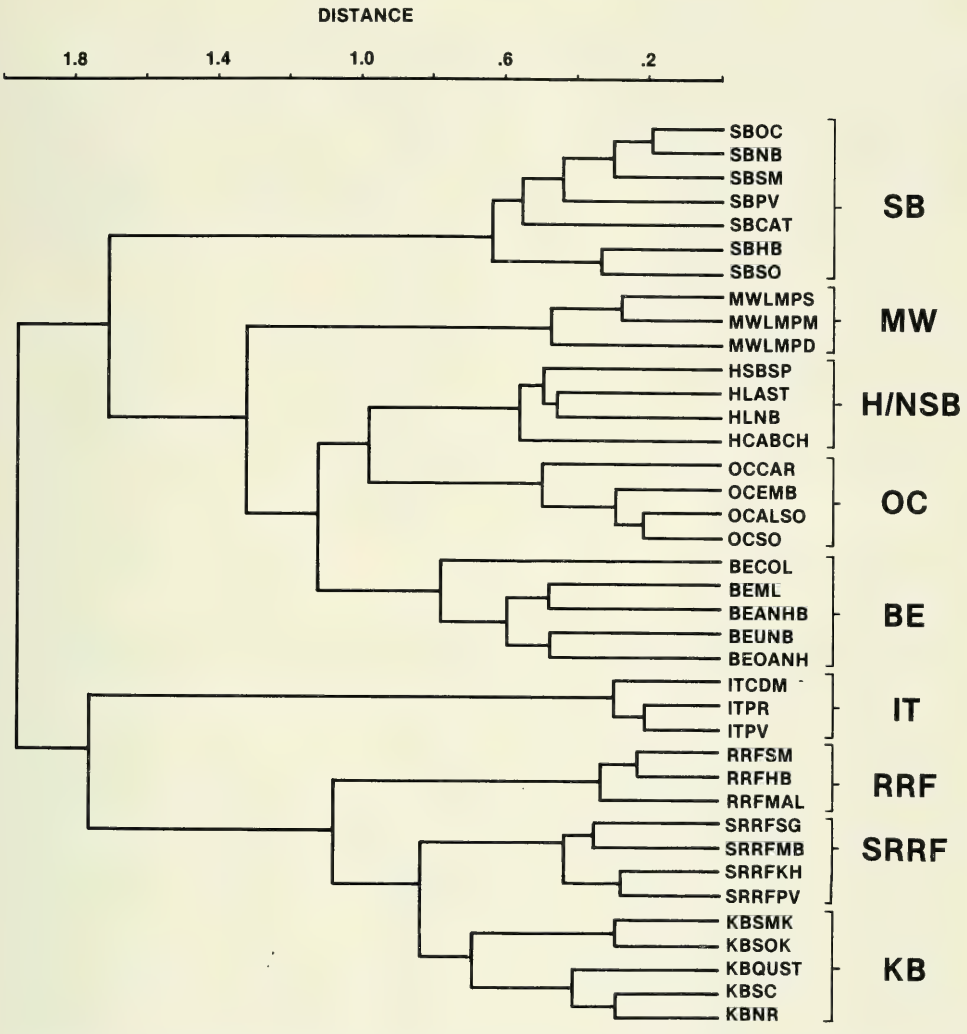

Fig. 2. Dendrogram of relationships between habitat sites from the cluster analysis using the Bray-Curtis Index of Dissimilarity. Nine basic groups are: SB = offshore soft bottom, MW = nearshore midwater, H/NSB = harbor/nearshore soft bottom, OC = open coast sandy beach, BE = bay and estuary, IT = rocky intertidal, RRF = deeper rock reef, SRRF = shallow rock reef, and KB = kelp bed.

to the overall value of either index (indices are based on the summation of natural logarithms of proportions).

Results

Habitat and Species Classifications

The 38 different habitat sites clustered into nine major habitats (Fig. 2) designated as SB (soft bottom-offshore), MW (nearshore midwater), H/NSB (harbor/nearshore soft bottom), OC (open coast sandy beach), BE (bay and estuary), IT (rocky intertidal), RRF (deep rock reef), SRRF (shallow rock reef), and KB (kelp

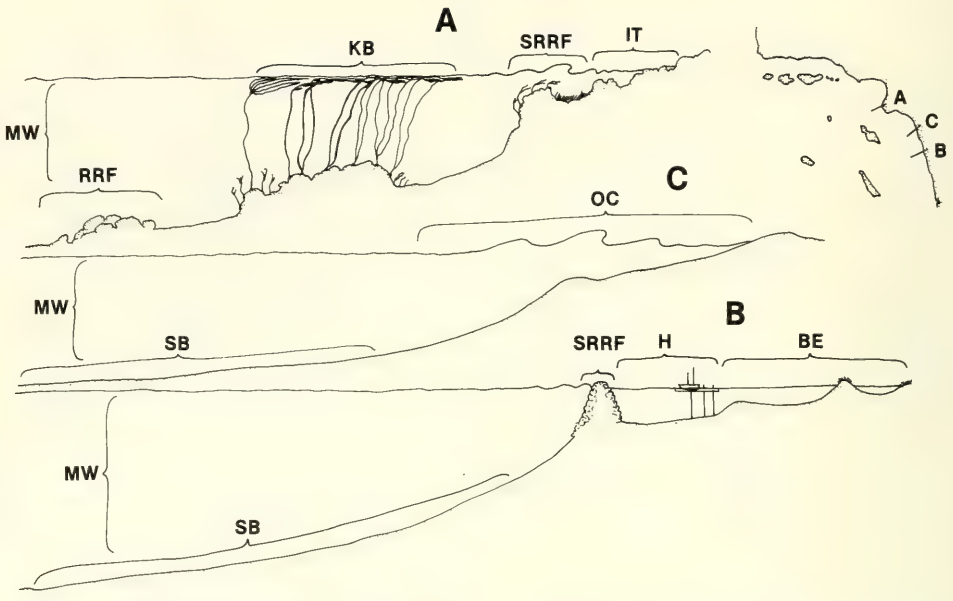

Fig. 3. Representative profiles of three transects (A, B, and C) from shore in the Southern California Bight depicting the relative placements of the nine habitat types derived from cluster analysis. Note that harbor breakwaters and jetties fall into the SRRF type. Other information as in Figure 2.

bed) (Fig. 3). These nine habitat types clustered into two major groups based on their respective fish assemblages, those associated with soft substrates and those with rock substrates. Of the five major habitats with soft substrates, the H/NSB and OC had the closest affinity. BE was next in similarity to the H/NSB-OC group followed by MW. The SB habitat was fairly unique and was far removed from the remainder of the soft substrate types. The KB and SRRF types had the highest similarity (lowest distance) among the four major rock substrate habitats. RRF was next in terms of similarity, followed by IT. Physically, the rock substrate habitats were segregated according to depth and distance offshore. The IT habitat was restricted to the rocky intertidal and adjacent shallow subtidal areas. SRRF habitats were located close to shore at depths between (approximately) 2–12 m. KB habitats were more offshore at depths between 8–18 m, while RRF were at depths >20 m. These depth limits only apply to the sites utilized in this analysis and should not be interpreted as definite boundaries between all such habitats in the Southern California Bight. Harbor breakwaters and jetties were classified as SRRF habitats.

The 105 species used in the analysis clustered into 19 distinct species groups (Fig. 4). The 105 species within these groupings represent the most common or conspicuous members of the assemblages within the major types of habitats. The species groups in numerical order vary from rock associated groups (i.e., I–V), to groups with more widespread occurrence across major habitats (i.e., VI–IX), to groups (with few exceptions) whose species were primarily restricted to soft substrate habitats (i.e., X–XIX) (Table 2).

Species Group I contained four species of fish which were restricted to the rocky intertidal (IT) habitat and adjacent subtidal areas.

Fig. 4. Species groups derived from cluster analysis utilizing the Bray-Curtis Index of Dissimilarity. Species groups are enclosed by brackets. This figure will act as the legend for drawings of species in the following habitat scenes (see Figs. 5–10).

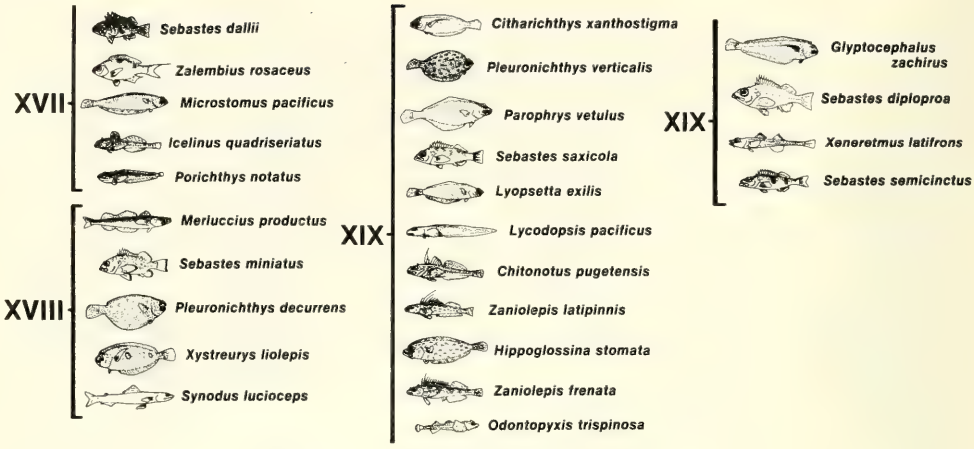

Fig. 4. Cont.

Species Group II consisted of three species which occurred in all rocky habitats, but were abundant as juveniles in the IT and SRRF habitats.

Species Groups III, IV and V included fishes almost exclusively associated with the SRRF, KB and, to a lesser extent, RRF habitat types. Group III contained six species which occurred in greater abundance in northern bight reef areas (*Hypsypops rubicundus* only at Santa Cruz Island) or the deeper portions of southern reefs. Group IV included four species which are almost exclusively associated with southern SRRF and KB habitats in the bight. Group V was made up of 10 species which were, with the exception of *Brachyistius frenatus,* widespread in all three (SRRF, RRF, and KB) Southern California rock reef habitats. *Sebastes carnatus* of Species Group III represented a composite of *S. carnatus* and *S. chrysomelas* in several habitats due to the difficulty of distinguishing them in the field (Ebeling, Larson, Alevizon, and Bray 1980).

Species Group VI was composed of four species of ubiquitous fishes. The three surfperches and one seabass occurred in most major habitats, especially those with a combination of soft and hard substrates.

Species Group VII contained two species of midwater (nearshore pelagic) fishes which were reported to be loosely associated with RRF and KB habitats probably at particular times of the year.

Species Group VIII included two subgroups of two species each and was somewhat artificial reflecting the limitations of clustering pooled, quantitative data. The species were reported in relatively low abundance across a wide range of nearshore habitats. Two of the species were closely associated with algal substrate, while the remaining two were associated with open water within the habitats.

Species Group IX was made up of six species of abundant habitat generalists. These species were numerically dominant in virtually all soft substrate habitats and were conspicuously less abundant in the KB and RRF habitat types.

Species Group X consisted of five species (including three croakers) restricted largely to open coast sandy beach habitats with sporadic/seasonal occurrence in BE and MW habitats.

Species Group XI represented a grouping of three nearshore pelagic species only encountered in the MW habitat samples.

Table 2. Summary two-way table of occurrence between species groups and habitat groups derived from cluster analysis. In order for a species group to be recorded as occurring within a habitat group, member species had to have a minimum total occurrence (across species) of 25 percent with all sites in the habitat group.

	Habitat groups								
Species groups	SB	MW	H/NSB	OC	BE	IT	RRF	SRRF	KB
I						*			
II						*	*	*	*
III								*	*
IV		*						*	*
V							*	*	*
VI	*	*	*	*	*		*	*	*
VII		*					*		*
VIII		*	*	*		*		*	*
IX	*	*	*	*	*			*	
X		*		*	*				
XI		*							
XII					*				
XIII			*		*				
XIV			*	*	*				
XV	*		*		*				
XVI	*		*				*		
XVII	*		*						
XVIII	*		*						
XIX	*								

Species Group XII contained six species which are indigenous to the BE habitat type.

Species Group XIII included four common BE species which also occurred in low abundance in harbor habitats.

Species Group XIV was composed of four species which occurred in relatively low abundance in shallow, nearshore habitats such as BE, OC, and H/NSB.

Species Group XV was made up of six species of benthic fishes most abundant in the H/NSB habitat type and to a much lesser degree in the BE habitat type.

Species Group XVI included four species which may be described as sand-rock bottom (ecotonal) fishes. They were reported from RRF and KB habitats and were also regularly recorded in otter trawl samples from the SB habitats.

Species Groups XVII, XVIII, and XIX were made up of species associated almost exclusively with the SB habitat type. Group XVII contained 10 species of numerically dominant, soft bottom (SB) fishes. This group included both the abundant shallow (H/NSB) and deeper water forms. The two cusk-eels, *Ophidion scrippsae* and *Chilara taylori* were very abundant only in the SB studies which included night sampling. Group XVIII contained five species of uncommon to rare SB fishes. Group XIX included 15 species of fish which were intermediate in abundance to those members in groups XVII and XVIII.

To further elucidate the relationships between the species groups and habitat types derived from cluster analysis, the occurrences of species groups within the major habitats are illustrated in Figs. 5–10. These illustrations are arranged first by rock substrate types, shallow to deep (Figs. 5 and 6) followed by soft substrate types, shallow to deep (Figs. 7–10). Particular members of a group are included

Fig. 5. Schematic diagram of species and species groups within the rocky intertidal (IT) and shallow rock reef (SRRF) habitats. See Figure 4 for the names of species that accompany drawings. Species groups are enclosed by dashed lines.

only if they had at least a 25% occurrence among the individual habitats of the major habitat in question.

Patterns of Diversity

Clearcut patterns of species richness (S) among habitats were obscured due to the aforementioned dependence of duration of the study on S (Table 3). These

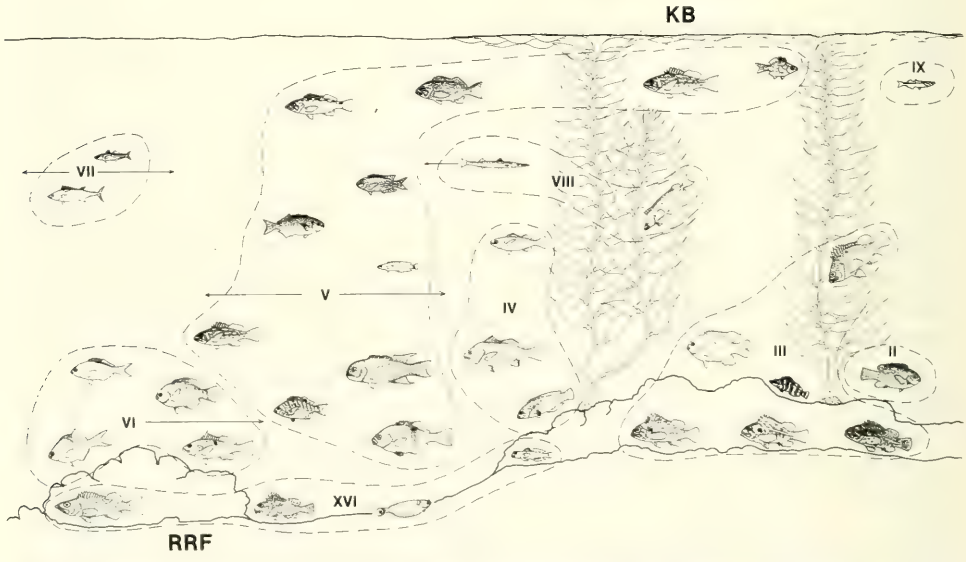

Fig. 6. Schematic diagram of species and species groups within the kelp bed (KB) and deeper rock reef (RRF) habitats. See Figure 4 for names of species. Species groups are enclosed by dashed lines. Arrows indicate occurrence in both habitat types.

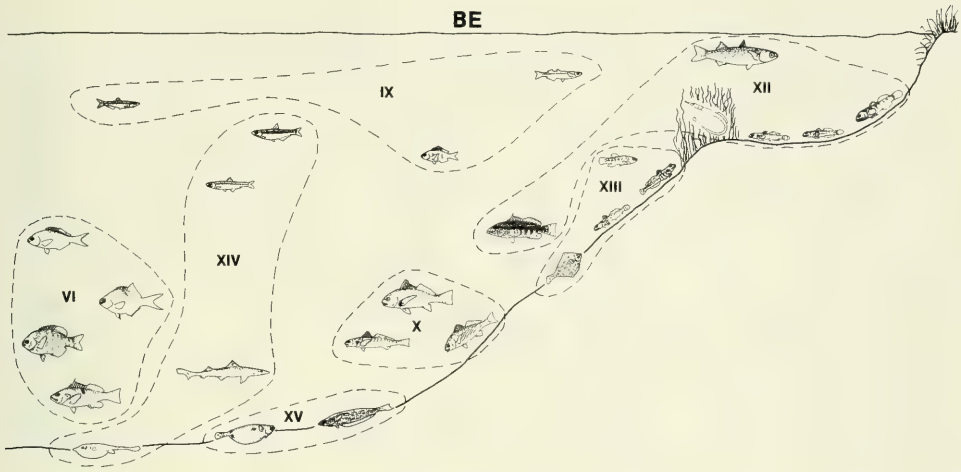

Fig. 7. Schematic diagram of species and species groups within the bay and estuary (BE) habitat. Other information as in Figure 5.

data are presented mainly for the sake of completeness and must be interpreted with caution.

Patterns of cumulative abundance among the top 10 species within the designated habitats ranged from sharply asymptotic (MW, BE, and IT) to gently sloping (RRF, KB, and SB) (Fig. 11). The H/NSB, OC, and SRRF habitats varied greatly among particular studies, but, in general, were intermediate in cumulative abundance. The sharp inclines in the MW, BE, and IT curves correspond to high numerical dominance by a few species in each assemblage. Correspondingly, gradual slopes in the curves of RRF, KB, and SB indicate a greater equitability or "evenness" in species abundances among the most common species in the assemblage.

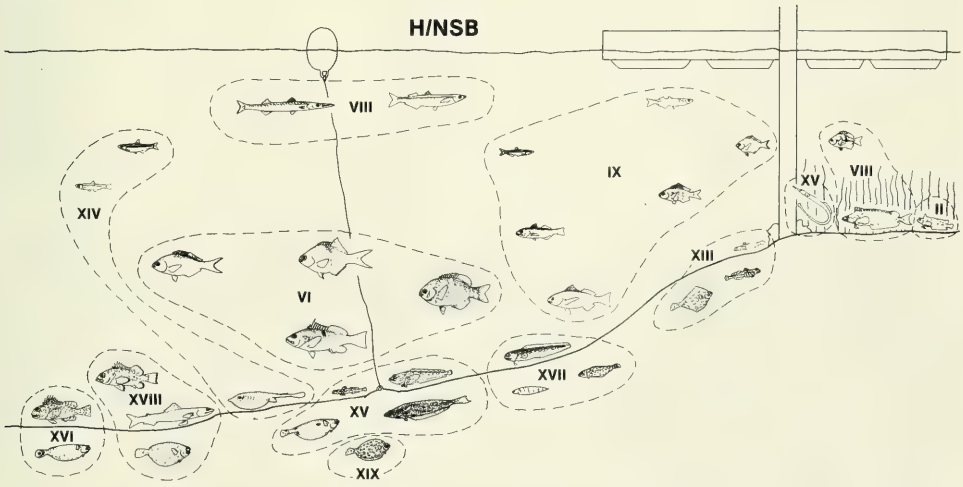

Fig. 8. Schematic diagram of species and species groups within the harbor/nearshore soft bottom (H/NSB) habitat. Other information as in Figure 5.

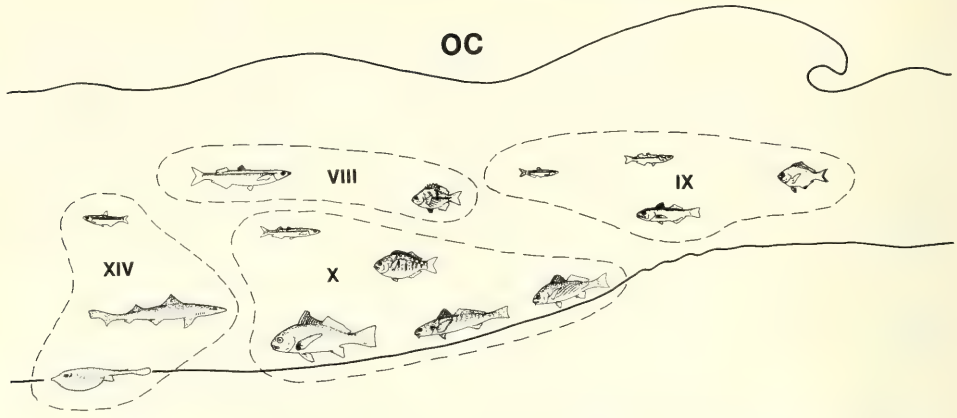

Fig. 9. Schematic diagram of species and species groups within the open coast sandy beach (OC) habitat. Other information as in Figure 5.

One factor that confounds the interpretation of the relative diversities of the fishes among the RRF, KB, and SB habitats is that, with few exceptions, the summary data for all SB habitats included the catches from a wide range of depths. It is not unreasonable to assume that over a depth gradient of as much as 125 m, depth replacement of assemblages occurs (e.g., see M. Allen 1982). Thus, the "diversities" of the SB habitats were artificially inflated by the inclusion of several assemblages within single samples. Catch data from discrete depths representing different subjective assemblages in the SBPV study were available to examine this problem. If shallow (S; 20–25 m), mid-depth (M; 60–62 m), and deep (D; 135–

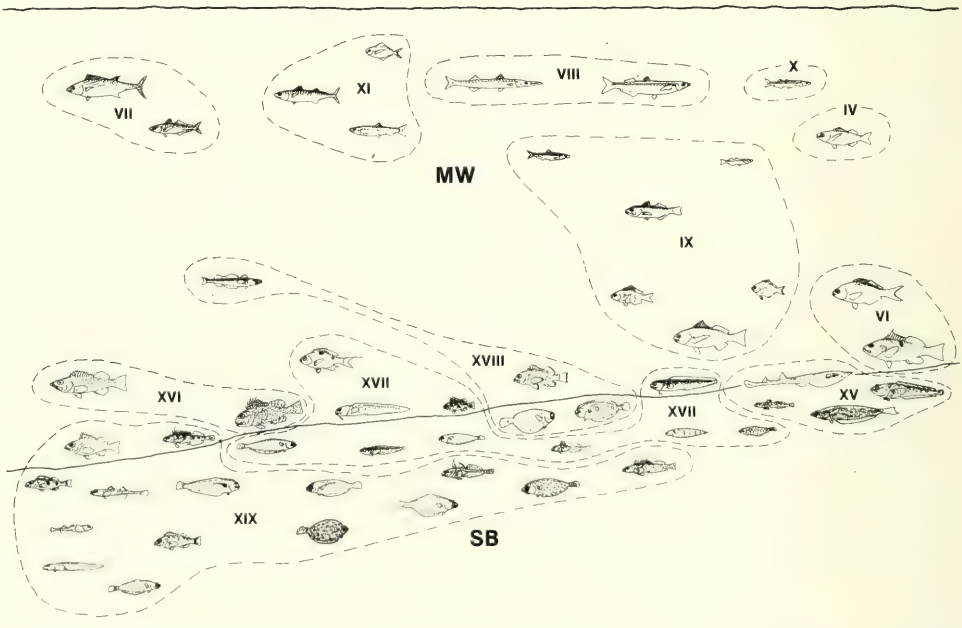

Fig. 10. Schematic diagram of species and species groups within the nearshore midwater (MW) and offshore soft bottom (SB) habitats. Other information as in Figure 5.

Table 3. Species richness (S = number of species making up >0.1% of total numbers), H′ and J′ diversity values, and mean species richness ($\bar{X}S \pm 1$ standard deviation) of the 35 study sites used in the analysis of diversity patterns. See table 1 for the meaning of abbreviations of sites.

Site	S	H′	J′	$\bar{X}S \pm$ S.D.
BECOL	7	0.46	0.19	
BEML	19	1.54	0.52	16.7 ± 6.6
BEOAB	22	1.01	0.33	
BEUNB	19	1.03	0.35	
HCAB	23	1.64	0.52	
HLAST	19	1.59	0.54	25.2 ± 5.2
HLNB	29	2.46	0.72	
HSBSP	30	2.20	0.65	
ITCDM	8	1.54	0.74	
ITPR	12	1.49	0.63	16.0 ± 10.6
ITPV	28	1.79	0.54	
KBNR	22	2.23	0.72	
KBSC	21	2.30	0.75	20.0 ± 1.8
KBSMK	18	1.67	0.58	
KBSOK	19	2.27	0.77	
MWLMPD	7	0.37	0.13	
MWLMPM	9	0.68	0.24	7.7 ± 1.1
MWLMPS	7	0.87	0.29	
OCAL	13	1.83	0.71	
OCCAR	28	2.23	0.67	22.2 ± 6.5
OCEMB	25	2.16	0.67	
OCSO	23	1.92	0.61	
RRFHB	21	2.16	0.71	
RRFMAL	17	2.19	0.77	19.7 ± 2.3
RRFSM	21	2.11	0.69	
SBHB	35	2.77	0.78	
SBNB	33	2.74	0.79	
SBOC	37	2.72	0.75	35.0 ± 3.6
SBPV	41	2.64	0.71	
SBSM	33	2.34	0.67	
SBSO	31	2.29	0.67	
SRRFKH	36	2.61	0.72	
SRRFMB	22	1.79	0.58	26.0 ± 8.7
SRRFPV	23	1.94	0.51	
SRRFSG	20	1.55	0.53	

150 m) trawls are summarized separately, the individual curves rise more sharply than the curve for the total sample (Fig. 12). This implies that the curves for SB habitats which include a wide range of depths are artificially depressed. Therefore, the diversity of SB habitats should be interpreted with caution. The curves of the individual depth strata at SBPV (Fig. 12) are, nonetheless, similar to those of the KB and RRF types which indicates that the SB habitat probably has a similar pattern of diversity.

Ranking the habitats based on mean value of H′ and J′ (Fig. 13) yielded patterns of diversity very similar to those found by examining cumulative abundance. The MW (H′ = 0.64; J′ = 0.22) and BE (1.01; 0.35) types ranked lowest in both H′

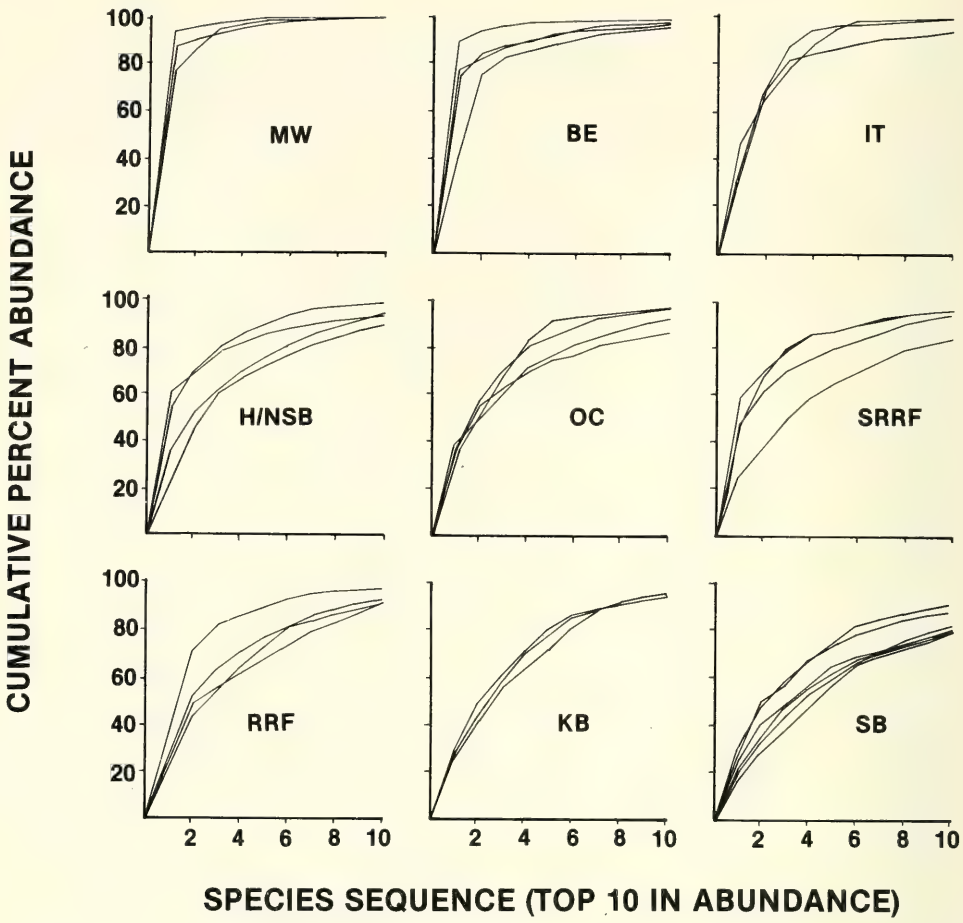

Fig. 11. Cumulative abundance curves of the top ten species in abundance (ranked) for each individual study site within the nine major habitats. See Figure 2 for names of habitats.

and J′ (IT ranked low in H′ at 1.61), while KB (2.12; 0.70), RRF (2.15; 0.72) and SB (2.58; 0.73) ranked highest in both indices. The similarity between the patterns of H′ and J′ indicates that the observed diversity was more strongly influenced by the evenness component than the species richness component.

H′ diversity was significantly correlated (Spearman rank correlation, $P < .05$) with sample size only in the IT sites. Neither the number of sampling methods employed nor the sampling intensity (samples/month) were correlated with H′ values within the major habitats. However, care must be taken in interpreting the results of rank correlations since sample sizes were small (N = 3–6) and power was very low.

Discussion

Affinities of Habitat Types

Among the rock substrate habitats, KB and SRRF exhibited the greatest similarity in species composition. This was probably due to the similarity in substrate type and the occurrence of structure forming algae in both habitats. Common

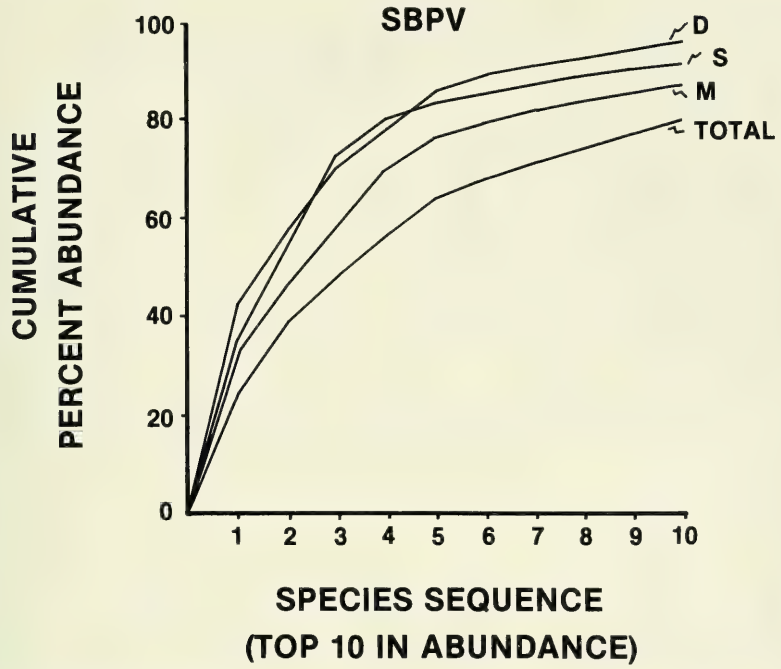

Fig. 12. Cumulative abundance curves for the top ten most abundant species at the soft bottom Palos Verdes (SBPV) study site broken into shallow (S), mid-depth (M) and deep (D) trawls. Total curve was derived from the combination of all trawls regardless of depth.

species in both types included members of Species Groups II–VI and VIII. The RRF habitats lacked Species Groups III, IV, and VIII. These omissions plus the absence of kelp-water column oriented fishes (e.g., *Brachyistius frenatus, Sebastes mystinus,* and *S. serranoides*) were largely responsible for the dissimilarity between the RRF and the SRRF/KB habitats in this analysis. The IT habitats were by far the most dissimilar of the rock substrate types owing to the unique species in Group I. Members of Species Group II occurred in the IT as juveniles (*Girella nigricans* and *Scorpaenichthys marmoratus*) or as a seasonal component (*Gibbonsia elegans*). The species in Groups II and VIII linked the IT to the SRRF habitat types.

Study sites within the KB and SRRF types exhibited similarities related to latitudinal proximity (regionalization) and differences in rock substrate type. KB and SRRF sites in the northern bight (i.e., KBSC, KBNR, SRRFKH, and SRRFPV) contained "northern" elements such as the rockfishes (*Sebastes* spp.) and *Oxylebius pictus* in Species Group III and *Sebastes mystinus* and *S. serranoides* from Species Group V (Ebeling et al. 1980). Conversely, southern sites (i.e., KBSOK, KBSMK, SRRFSSG, and SRRFMB) contained more species with southern affinities such as the members of Species Group IV (*Xenistius californiensis, Cheilotrema saturnum, Halichoeres semicinctus* and *Anisotremus davidsoni*). The kelp bed habitats at KBSOK and KBSMK differed in substrate type from the other KB sites. These particular southern kelp beds have cobble substrates (Larson and DeMartini in press). Cobble substrates do not afford suitable shelter sites for many shelter seeking species (Larson and DeMartini in press), such as *Chromis punc-*

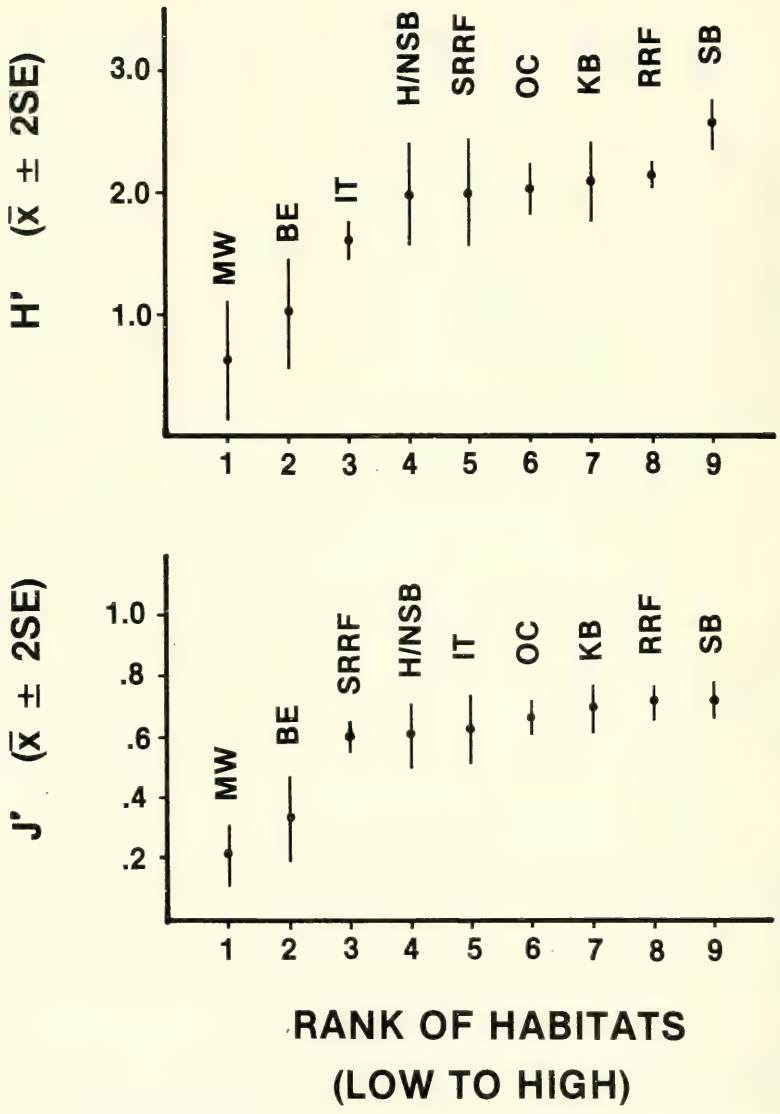

Fig. 13. Mean H′ diversity (top) and J′ evenness (bottom) values for the nine major habitats ranked from low to high. Vertical bars represent ±2 standard errors (SE). See Figure 2 for names of habitat types.

tipinnis (of Group V), *Hypsypops rubicundus* (rare at KBSMK and absent at KBSOK), *Sebastes rastrelliger, S. auriculatus,* and *S. carnatus* (of Group II). Lack of shelter sites probably accounts for the relative rarity of these species at KBSOK and KBSMK (E. E. DeMartini pers. commun.). Most of these species were abundant in the KBQUST sites that were on high-relief rock substrates, farther south in the bight.

All studies within the KB, SRRF and RRF habitat types were based on diver transects or observations and did not consider the cryptic species.

The OC and H/NSB habitat types were most similar among the soft substrate

types and shared species, most notably, from Groups VI, VII, IX and XIV. The BE habitats exhibited a fairly close affinity to both the OC and H/NSB mainly due to the shared occurrence of Species Groups VI, IX and XIV (shared by all three) and Group X (shared between BE and OC). Species within Group X are residents of the OC habitat which occur seasonally (spring–summer) within the BE environment. BE maintains its distinctiveness from other soft substrate habitats by virtue of the unique species within Groups XII and XIII. Both groups contained species which are virtually indigenous to the bays and estuaries in Southern California (e.g., longjaw mudsucker, *Gillichthys mirabilis*; shadow goby, *Quietula ycauda*; California killifish, *Fundulus parvipinnis*; and striped mullet, *Mugil cephalus*). The MW habitat type shared several groups with the OC-H/NSB-BE complex including Groups IX and X. Groups VII and XI were unique to the MW realm (Allen and DeMartini 1983) although members of Group VII were also associated with reefs and kelp beds at some time of the year (present study and Feder, Turner, and Limbaugh 1974). The SB habitat was the most distinctive of the soft substrate habitats. Although the SB sites shared some groups of shallow species (Groups XV and some species in XVII) with the H/NSB and OC habitats it remained unique due to the particular assemblage of fishes represented in Groups XVII (most members), XVIII and XIX.

The observed, general similarity between rock and soft substrate habitats was due to the occurrence of particular species (principally within Species Groups VI, VIII, IX and XVI) in a wide range of habitats.

Species Groups: Habitat Generalists and Specialists

The 19 species groups can be broken down into subsets which exhibited both widespread (generalized) and restricted (specialized) distributions among major habitats. An examination of some of the general morphological, physiological and life history characteristics of generalized and specialized species follows. In keeping with the established order of species group numbering, rock substrate specialists will be examined first, followed by habitat generalists and soft substrate specialists.

Rock habitat specialists were clustered into Species Groups I–V. Important perciform families included the Embiotocidae, Labridae, Pomacentridae, Haemulidae, Clinidae, and Kyphosidae. The Scorpaenidae (genus *Sebastes*) and Cottidae were the conspicuous scorpaeniform representatives. Virtually all of the rock substrate specialists are cryptically colored. Many species are territorial during some part of their life history (e.g., Clarke 1970; DeMartini and Anderson 1980; Hixon 1980; Larson 1980).

Species Group I was restricted to the IT habitat type and the members have both morphological and physiological adaptations for living in a turbulent and physiologically stressful environment. All four species are adapted for dwelling in holes and under rocks. The clingfish (*Gobiesox rhessodon*) clings to rocks using its thoracic suction disc. These IT species tolerate wide ranges of temperature, salinity, and dissolved oxygen levels. Several (*Gobiesox rhessodon, Paraclinus integripinnis* and *Clinocottus analis*) are suspected air breathers (Congelton 1980 and pers. obs.).

The habitat generalists in this study may be divided into two main groups, those which are widespread across both rock and soft substrates and those which are widespread over various types of soft substrates.

Rock and soft substrate generalists included species in Groups VI and VIII. Perciform families include the Embiotocidae (four species), Serranidae, Sphyraenidae, and Clinidae. The one non-perciform member of the subset belongs to the Atherinidae. The species in this subset (species Groups VI and VIII) exhibit both cryptic coloration and countershading, as well as laterally compressed and elongate, fusiform body shapes. Species such as *Embiotoca jacksoni, Micrometrus minimus,* and *Heterostichus rostratus,* which are laterally compressed and cryptically colored, are mainly associated with rock substrate and/or kelp in a wide range of habitats. Laterally compressed, counter-shaded species such as *Phanerodon furcatus* and *Damalichthys vacca* are probably associated with soft and rock substrate habitats. The elongate, fusiform, and countershaded species (*Sphyraena argentea* and *Atherinopsis californiensis*) occur in the water column in a variety of habitats.

Species in Group XVI also occurred in both rock and soft substrate habitats. This group seemed to occur in areas of interface between rock and soft substrate types, and was primarily associated with the SB and RRF habitats. All four species are cryptically colored.

Soft substrate generalists in this analysis included the species of Group IX. This group occurred across all soft substrate habitat types and in the SRRF habitat. All of these species are strikingly countershaded. Four of the six species are approximately fusiform in body shape with the two surfperches, *Hyperprosopon argenteum* and *Cymatogaster aggregata,* being the exceptions. All species occupy the water column in many habitats although *Genyonemus lineatus* (and to a lesser extent *C. aggregata*) are more demersally oriented than the other members of the group (Allen and DeMartini 1983). All species are largely planktivorous in their feeding habits. *Engraulis mordax, Hyperprosopon argenteum,* and *Seriphus politus* are planktivorous throughout their lives (although large adult *S. politus* are piscivorous) with the latter two species feeding mainly at night (Hobson and Chess 1976; Allen and DeMartini 1983). *Atherinops affinis* is mainly planktivorous in its younger stages, but, depending on habitat, may also be omnivorous (Quast 1968) or even herbivorous (Allen 1980). *C. aggregata* (Hobson, McFarland, and Chess 1981) and *G. lineatus* (Phillips, Terry, and Stephens 1972) are planktivores when young and become benthic feeders when older. All six species in Group IX are usually very abundant in the habitats in which they occur. All appear to have high reproductive output (except *Cymatogaster aggregata*) and relatively short lives.

Even though the soft substrate habitats overlapped greatly in their species assemblages, soft substrate specialists were identified in the analysis. Such groups occurred in OC, MW, BE, and SB habitat types.

The open coast (OC) sandy beach environment is occupied by a unique set of species in the members of Group X, although some members occurred seasonally (spring–summer) in BE and MW habitats. All species are countershaded with varying degrees of cryptic coloration (vertical bars or oblique stripes). The three sciaenids (*Umbrina roncador, Roncador stearnsi,* and *Menticirrhus undulatus*) and the embiotocid (*Amphisticus argenteus*) all possess either terminal to subterminal mouths for feeding on benthic invertebrates that occur in sandy substrates (Carlisle, Schott, and Abramson 1960). The remaining member, *Leuresthes tenuis,* possesses a tubular, protrusible jaw which is best adapted for planktivorous feed-

ing. Body forms were typical of water column (elongate fusiform—*L. tenuis*) and demersal species (moderate to strong lateral compression—*U. roncador* and *A. argenteus*).

The MW habitat type in Southern California contained many species of nearshore water column and demersal fishes, particularly those from Groups VI, VIII and IX. Species in Groups VII and XI are virtually exclusive to the coastal pelagic realm (Group VI, as previously mentioned, was also associated with rock reef habitats). All species are countershaded with silvery sides, and have fusiform bodies and deeply forked to lunate caudal fins. The latter two characters are widely recognized as adaptations for fast, nearly continuous swimming. The group as a whole contains generalized predators (planktivores and piscivores). Only *Peprilus simillimus* possesses a specialized feeding morphology (epibranchial organ) (Horn 1970). Allen and DeMartini (1983) presented a seasonal characterization of this MW habitat which was similar to the one presented here. In the previous study, members of Species Group IX were numerically dominant. Groups VI, X, XI, and *Sphyraena argentea* and *Atherinopsis californiensis* of Group VIII also were common members of the assemblage in their study.

Bay and Estuarine (BE) habitats possess distinctive elements within their fish faunas. A large number of seasonally migratory species, together with resident species indigenous to the BE habitat, were clustered into Groups XII and XIII. The benthic members are cryptically colored to blend with the substrate. The water column species, *Mugil cephalus,* is countershaded with disruptive lateral stripes. All except *Paralabrax maculatofasciatus* are low trophic level species that feed mainly on small invertebrates (Allen and Horn 1975; Allen 1980). *Mugil cephalus* is a herbivore/detritivore (Allen 1983). Most members of Groups XII and XIII are eurythermal and euryhaline in order to cope with this physiologically stressful environment (Haedrich and Hall 1976). Horn and Allen (1981) characterized the ichthyofauna of upper Newport Bay in 1978. Their residents were represented in Groups IX (*Atherinops affinis*), XII, XIII, and XV within the present analysis. Seasonal periodics are included in Species Groups X, XIV, and XV.

The SB habitat type possessed the most distinctive ichthyofauna among the soft substrate habitats. SB specialist species are included in Groups XV–XIX. Eight orders of fishes are represented in this subset (Pleuronectiformes, Scorpaeniformes, Perciformes, Batrachoidiformes, Gasterosteiformes, Myctophiformes, and Rajiiformes) which is by far the most in any one type of habitat. Virtually all of the SB species have cryptic coloration, especially those which are closely associated with the bottom. Demersal fishes which spend time above the bottom tend to be countershaded (e.g., *Zalembius rosaceus* and *Merluccius productus*). Body forms include flatfish type (laterally compressed laying on one side, bothids and pleuronectids), eel-type (ophidiids and zoarcids), dorso-ventrally compressed (cottids, agonids, and batrachoidids), and robust types (scorpaenids). Feeding specializations and depth stratification in distributions are prominent within this subset of groups. It is important to re-emphasize, at this point, that the nature of this analysis prevented any resolution of SB species groups based on factors other than numerical abundance. Therefore, the species grouping may not reflect strict ecological relationships in a few cases. M. J. Allen (1982) analyzed in detail the depth replacement, recurrent groups, and feeding specializations within the soft bottom fish assemblages off Southern California.

Certain families exhibited great flexibility in habitat requirements, occurring across a wide range of habitat types. Surfperches (Embiotocidae) occurred in all nine habitat types. Croakers (Sciaenidae) were represented in seven major habitats. Silversides (Atherinidae) and seabasses (Serranidae) were found in six habitats, followed by scorpionfish and rockfishes (Scorpaenidae), gobies (Gobiidae), and right-eyed flatfishes (Pleuronectidae) in five; and sculpins (Cottidae), kelpfishes (Clinidae), barracuda (Sphyraenidae), and sea chubs (Kyphosidae) in four habitats each.

On the other hand, some families were restricted to only one type of habitat. These restricted families and their habitat were as follows: Gobiesocidae and Blenniidae (IT); Mugilidae and Cyprinodontidae (BE); Synodontidae (H/NSB); Clupeidae and Stromateidae (MW); and Agonidae, Zoarcidae, Rhinobatidae, and Merluccidae (SB).

The vast majority of fish species encountered in the marine habitats of Southern California belonged to the superorder Acanthopterygii. Prominent orders of acanthopterygian fishes included the Pleuronectiformes, Scorpaeniformes and, especially, the Perciformes. Perciform fishes were dominant or well represented in every major habitat attesting to the amazing adaptability of these highly derived bony fishes. Perciform fishes ranged in body form and habits from dorso-ventrally flattened, benthic, hole dwelling forms like blennies and gobies to laterally-compressed, demersally orientated forms like surfperches (Embiotocidae), croakers (Sciaenidae), and seabasses (Serranidae) to fusiform, midwater swimmers like bonita, mackerel (Scombridae), and jacks (Carangidae).

In general, perciform and to a lesser degree scorpaeniform fishes dominated in rock substrate habitats. Members of these orders possess the derived acanthopterygian characteristics of fin spines, ctenoid scales (unless secondarily lost), protrusible jaws and, in basal members, deepened, laterally compressed bodies. Fin spines and ctenoid scales may offer protection from predators as well as from abrasion on rocks. The deepened body with thoracic pelvic fins and pectorals high on the sides of the fish (particularly in basal perciform fishes) represent adaptations for efficient maneuverability in close quarters. Protrusible jaws were prerequisite for the tremendous diversification of feeding strategies seen among these species (Moyle and Cech 1982, p. 192–193).

Pleuronectiform fishes dominated the soft substrate habitats (particularly the SB). These fishes are highly specialized to a benthic existence by having both eyes on one side, laying on the other side and having extensive color and pattern change capabilities. Cryptically colored, scorpaeniform fishes were also well represented in soft substrate habitats.

Open water within habitats was occupied, principally by Atheriniform, Clupeiform, and Perciform fishes. Major adaptations of these water column fishes included elongate, streamlined, or fusiform body shapes. All are relatively fast swimmers which exhibit marked countershading.

Patterns of Diversity

The nine major habitats fell into three general levels of species diversity; those of relatively high (KB, RRF, and SB), medium (OC, SRRF, and H/NSB), and low (BE, IT, and MW) species diversity. Two basically different environments were represented among the high diversity habitats. The KB and RRF types were similar due to their heterogeneous rock substrate, whereas the SB habitat possessed

a relatively homogeneous soft substrate. The low diversity habitats included two physically stressful environments (BE and IT) and one which is probably physically variable due to patchy resources, shifting water masses and unpredictable bouts of upwelling (MW).

According to the data presented herein, the diversity of the SB habitat appears to be higher than the diversity of both the KB and RRF habitats (see Figs. 11 and 13). However, as discussed earlier, H′ values of most SB sites were probably inflated artificially to some degree by the inclusion of several depth strata into one sample. Separation of depth strata (as with SBPV, Fig. 12) indicated that SB, KB, and RRF habitats were generally comparable in fish diversity. Another factor must be considered, however. Proportionately more species of cryptic fishes are probably captured in trawl samples from SB sites than are censused by divers in KB and RRF sites. The potential impact of the addition of these cryptic species on both H′ and J′ diversities is unclear. Conceivably, though, an increase in these values could place both the KB and RRF above the SB habitats in species diversity. The escapement of large, strong swimmers from trawl samples in SB sites probably has little effect on H′ and J′ diversities since large fishes are usually rare.

No clear-cut explanation for the observed pattern of diversity is apparent, but the following is offered in the hope of stimulating further discussion on the subject. One possible explanation for these observed patterns is that MW, BE, and IT habitats may be similar in terms of low physical constancy (high variability). All three could be viewed as physically unpredictable environments which support only a few "tolerant" species. The KB, RRF, and SB habitats would, in this scenario, represent relatively predictable or constant environments which support a greater diversity of fishes. High diversity in the KB, RRF, and SB habitats may simply reflect niche diversification within these three environments. Niche diversification in the relatively homogeneous SB habitat would have to be subtle and take the form of resource partitioning along food, space, and time dimensions (Pianka 1978). Two alternate explanations for the apparent high diversity in the SB habitat also exist. The first was originally proposed by Sale (1978) to explain the high diversity of fishes on coral reefs. The high diversity of fishes in the SB habitat, according to this view, could be due to random factors in colonization which create a mosaic of overlapping distributions among SB species (chaotic view). The second explanation is based on sheer size of the habitat. The SB habitat (along with MW) covers the largest area by far among the southern California habitats. The SB habitat may, simply, owe its large number of fish species and high H′ diversity to its large area.

Any model incorporating habitat heterogeneity would have to reconcile how a habitat with a relatively homogeneous substrate (SB) can hold an assemblage of fishes which may be as diverse as those of habitats with highly heterogeneous substrate (KB and RRF).

This analysis points to two glaring deficiencies in our knowledge of fishes and their habitats off southern California. The first is the lack of good quantitative data on the physical and chemical characteristics of the major habitats. Secondly, the omission of cryptic species from diver censuses in rock substrate habitats makes it impossible, at this time, to determine fish diversity with accuracy. The patterns of diversity among nearshore fishes within the Southern California Bight will remain somewhat unclear until these questions are answered by future investigations.

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The Nest of *Tracheliodes foveolineatus* (Viereck), and Normal Reversal of Cocoon Orientation Within it (Hymenoptera: Sphecidae: Crabroninae)

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The nest, prey, cocoon, curious inverse orientation of the cocoon, and some other aspects of the biology of *Tracheliodes foveolineatus,* an ant-predator, are described, analysed, and compared with relevant features of other Nearctic and Palearctic species of *Tracheliodes.* Species specificity of prey and wasp is discussed, as are some problems associated with the communal cells made by these wasps.

Parker and Bohart (1966) recorded occupation of elder trap nests by the ant predator, *Tracheliodes foveolineatus* (Viereck), but the account now to be given provides for the first description of the nest and relevant biology. The nest of this species is remarkably like that of *T.* (? *amu* Pate, or new species) described in detail by Krombein (1967). Krombein's account, along with those of the nests of the two Palearctic species by Ferton, Emery, and Grandi, to be considered in the discussion, make possible a useful comparison of aspects of the biology of four of the five known living members of *Tracheliodes,* and at least one surprising inference.

The Nest and Cocoon

The wasp *Tracheliodes foveolineatus* (Viereck) founded a linear nest in an elder stem (16 mm in diameter, previously bored to a depth of 23.5 cm and width of 7.9 mm). On 27 July 1983, the trap was nailed about 1.5 m above ground, horizontally, to the trunk of a large oak standing in deep shade some 18–20 m from the outer shrubbed margin of a wood at Julian, San Diego County, California (1230 m in altitude). The nest was removed on 11 September and opened several days later. For reasons to be explained in the discussion, I shall refer to subdivisions of its bore provisioned with prey as "cells" or sets (of prey).

There were 12 "cells," plus an incomplete terminal set of prey open to the 10.3 cm long entrant passage. The "cells" commenced from the bottom of the burrow (=bore), averaged 11 mm in length (range 7–13 mm) and at least in part these had been marked off into "cells" by unconsolidated, small fragments of pith that formed flimsy boundaries, 1 mm or less in thickness. The evidence for such delimitation of the sets of prey, or "cells," consists of the definite but skimpy, transverse, thin aggregates of pith particles bounding the anterior margins of "cells" 10 (prey only) and 12 (prey plus collapsed egg), and the scattered particles adherent to the lengths and transverse faces of cocoons in the other ten "cells" (see below).

Some of the pale yellowish cocoons revealed the head of a fully colored adult

wasp at the abruptly flared end that faced the entrance to the burrow. At the flared end, cocoons terminated in a transverse, tough, parchment-like, flat disc affixed tightly to the wall of the burrow by a darkened rim about 0.8 mm wide. Behind that rim, cocoons tapered abruptly, becoming cylindrical about the long axis of their "cell," with the end directed toward the base of the nest smoothly rounded.

Seven measured cocoons had a mean length, of 7.7 mm (range 7–8.8 mm) from the transverse disc to the tip of the rounded end, a mean girth of the cylindrical portion of 3.3 mm (range 2.3–3.8 mm), with the diameter of the transverse disc necessarily equal to 7.9 mm (the diameter of the boring).

Most cocoons of this nest had either a scattering of remains of prey and fragments of pith against the outer face of the anterior wall, or fragments of pith affixed here and there along the length of the cocoon among the abundant remains of prey. Those particles of pith are probably the remains of the insubstantial septa left by the mother, demarcating sets of prey, and thereafter scattered by the cocooning larva.

The fabric of the cocoon did not contain foreign particles, nor was it coated with particles although cocoons of some crabronids do contain inclusions or are coated with them (see Hachfeld 1945). The 70 micron thick, tough disc that faced the entrance to the burrow consisted of a tight meshwork, with interstices but 4–5× the thickness of its finest fibers (from 10–20 microns thick). The fine mesh lay between the fibers of a much coarser network (resembling a retinal capillary-bed) made up of much thicker fibers (up to 80 microns wide, hence traversely flattened). In the abruptly tapered region behind the disc, fine fibers formed a tight, even, transitional network that expanded into a widely open, coarse mesh of irregularly thickened fibers along the length of the cocoon. The spaces of the coarser mesh were in turn filled by finer networks. The largest fibers in the mid-region of the cocoon exceeded 100 microns at their widest. As the thickness of the wall of the cocoon along its length was only 30–40 microns, these fibers are markedly flattened, and must then have been laid down upon the finer meshwork. From the outer surface of the cocoon, here and there at points below which the larger structural fibers of the wall lie, slender fibers 15–25 microns in diameter arose, forming an open, three-dimensional web that bound the length of the cocoon to the wall of the "cell." Enclosed within this web, encasing the length and rounded end of the cocoon, were the bodies and remains of prey, as well as occasional particles of pith. The blind end of the cocoon, facing the closed end of the burrow, was also formed of larger meshworks enclosing finer meshworks similar to those of the body of the cocoon, but overall somewhat less coarse. The entire inner surface of the cocoon was covered by a pliable, glistening, amber-colored secretion or "varnish" that filled the interstices of the meshworks and gave the overall yellowish color to the cocoon that contrasted with the whitish fibrils attaching the cocoon to the wall of the "cell."

The prey in the completed "cells" were counted from heads only. They totalled some 395 workers (from small to large) of *Liometopum occidentale occidentale* Emery, ranging from 20 in a "cell" 7 mm long to 42 in a 43 mm "cell," with a mean of 33 per completed set of provisions. There were an additional 7 prey in the terminal, incomplete 13th set, in which no egg had been laid. "Cell" 12, with 42 prey, had a collapsed egg (ca. 2 × 0.5 mm) of the wasp stuck by its anterior end to the fore margin of the right mesosternum immediately behind the procoxa,

at a right angle to the length of the ant's body. The egg-bearing ant was an intermediate-sized worker among the 5 or 6 ants nearest the base of the "cell." That "cell" was closed off behind by the pith-flecked disc of the cocoon of its older sib. No egg was found on any of the prey in "cell" 10, nor were any of its ants disarticulated. It is thus likely that eggs are laid only after some number of prey have been brought into a set of provisions.

The split nest was left, partially reassembled, within an emergence tube; on 19 September 1983, 2 males and 2 females emerged; 20 September, 4 females emerged. These emergences make it very likely that the nest had been abandoned or the mother had died, at least a fortnight or longer before the nest had been brought in on 11 September. A seventh female, that in "cell" 4, was dead, only partially ecdysed, somewhat dismembered, protruding head first from a long rent at the rounded end of her cocoon—probably a victim of butchery by one or both emerging siblings from "cells" 2 and 3.

As it is certain that "cell" 11 produced a female, this nest could not have possessed an unbroken sequence of females that commenced at the blind end of the burrow. Though adult wasps of both sexes possess "mite chambers" on the second to penultimate metasomal tergites, no mites have been found within them or within the nest. These acarinaria are wide, but very shallow and even with distension could harbor only exceedingly small mites, perhaps deutonymphs of a species of *Crabrovidia* (Fain 1973). Finally, the brood was parsivoltine (Torchio and Tepedino 1982), for the very base of the burrow contained a cocooned resting larva destined to transform to an adult in the spring or summer of 1984.

Discussion

All five of the living Holarctic species of *Tracheliodes* (an additional three are known as fossils, Leclerq 1954) are peculiar among crabronines by their exclusive predation upon workers of two genera of dolichoderine ants; thus upon:

Tapinoma erraticum (Latr.) and *T. nigerrimum* Nyl.	*Tracheliodes quinquenotatus* (Jurine)	(1)
Liometopum microcephalum (Panz.)	*T. curvitarsis* (Herr.-Schaeff.)	(2)
Liometopum sp. ?	*T. hicksi* Sandhouse	(3)
L. occidentale luctuosum Wheeler	*T.* (? *amu* Pate)	(4)
L. occidentale occidentale Emery and *L. occidentale luctuosum* Wheeler	*T. foveolineatus* (Viereck)	(5)

Records: for 1, Palearctic (Ferton 1890; Grandi 1928, 1961); for 2, Palearctic (Emery 1893); for 3, Nearctic (Hicks 1936); for 4, Nearctic (Krombein 1967); for 5, Nearctic (Parker and Bohart 1966, and this report). As to the identity of *T.* (? *amu*): Pate (1942) described *T. amu* from a single male specimen collected in New Mexico. Krombein's three reared specimens are females; as he states, they are either *T. amu* or a new species.

It is interesting that Pate (1942) correctly predicted that *L. occidentale* (originally described by Emery 1895, as a subspecies of the Palearctic *L. microcephalum*) would be found to be the prey of *T. foveolineatus*. However, he furthermore inferred what the prey of *T.* "*amu*" and *T. hicksi* might be (respectively, *L.*

apiculatum apiculatum Mayr and *L. apiculatum* [sic!] *luctuosum* Wheeler). Pate also considered the European records then available but ignored Grandi's (1928) listing, as Grandi then recorded it, of *Tapinoma erraticum nigerrimum* as prey of *T. quinquenotatus* at one locality. Pate then concluded that very likely no two species of *Tracheliodes* prey upon the same dolichoderine species or subspecies, and that each species of *Tracheliodes* is restricted to but one species or subspecies of ant. As can be seen from the tabulation of prey and hosts, both conclusions are false; nevertheless, the apparently invariate relation between species of *Tracheliodes* and dolichoderine ants is a significant one.

All of the extant Holarctic species of *Tracheliodes,* but *T. hicksi,* have something known of their nesting biology (review in Pate 1942). The four species of which nests have been found occupy empty burrows or crevices in walls of suitable length and diameter (4–8 mm) for their linear nests, and one of the four (*T. quinquenotatus*) is known to dig nests in sandy and other soils as well. Except for Krombein's (1967) inclusive account of the nest of *T. "amu,"* few significant details of nest structure have been recorded for the other species.

Like many other crabronines (Kohl 1915), *T. "amu"* and *T. foveolineatus* do not close off their entrant burrows; probably this is so for the Palearctic species as well, but Ferton, Emery, and Grandi make no mention of this, nor do they mention whether the burrows are divided into cells by transverse walls, barriers, or by "markers" of fill that offer no effective obstacle to passage, such as very short, transverse assemblages of unconsolidated dirt or wood particles.

The dolichoderine ants upon which *Tracheliodes* species prey are alike in being forms that run in files, in large numbers, day after day, on open ground and tree trunks, forming an abundant food resource for these wasps of specialized hunting habits. They provide an economical resource, as the search for prey is reduced to that preceding the initial discovery. Provisions per larva are similar in all four, *T. foveolineatus, T. "amu," T. curvitarsis,* and *T. quinquenotatus,* namely 25–40 ants more or less, lightly paralysed, and closely packed. Females lay their eggs within the lower third of each store of prey, near its base, on an ant as I have described for *T. foveolineatus,* and as has been noted for *T. curvitarsis* (Emery 1893) and described and figured for *T. quinquenotatus* by Ferton (1901, pl. 2, fig. 6; 1923, fig. 26) and Grandi (1961, fig. 130). As Pate (1942) points out, that location of the egg enables ". . . the newly hatched larva to find immediately a suitable place for attacking the soft tissues . . . ," namely through the conjunctival membrane just behind the fore coxae.

Krombein (1967) clearly showed that each of the four nests of *T. "amu"* contained but one communal cell. For *T. foveolineatus* I have given reasons to suppose that divisions (or "cells") were marked off by the mother using short clusters of unagglutinated pith particles (hence not firm barriers), namely debris not cleaned from the burrow by the drill. Though Ferton (1901, 1923), Emery (1893), and Grandi (1961) fail to mention whether or not the burrow of *T. quinquenotatus* is cross-partitioned, they do speak of individual cells. However, Grandi's (1961) account of an uninterrupted column of 94 prey in one burrow (sufficient for 2–3 larvae), and his suggestion that provisioning may first be completed and then eggs laid at intervals within the column of prey, imply a communal cell or at most weakly marked-out "cells" in which dividers offer little resistance to penetration by the mother. I suspect that where rented burrows occupied by species of *Tracheli-*

odes contain particulate debris, "cells" will be found to be marked out, but not by firm walls, and not as a requirement, but merely as an efficient means of disposing of the debris, keeping it from hindering feeding larvae.

Such isolation of small accumulations of pith particles transverse to a completed set of prey need call upon no new or novel behavior for these wasps. Crabroninae of many genera place loose fill from debris in the burrow, or scraped from its walls, or taken from elsewhere, as the anterior boundary of each cell. Almost certainly such instinctive behavior was among the practices expressed by ancestors of *Tracheliodes.* It may be viewed, then, as no more than an atavistic reaction and utilization of debris in the burrow on the part of *T. foveolineatus.* Absence of free particles of wood within the borings of Krombein's series of nests would be sufficient cause for the differences between those nests of *T.* "*amu*" and mine of *T. foveolineatus.* My elder stem traps, not thoroughly dried out before drilling, in no case gave debris-free borings. Even so, such loose cross-fill may not be detectable after cocoons have been spun. Cocooning larvae may remove the particles from the frail accumulations and include them within the envelope of debris that is formed about the cocoon, as indeed sometimes occurs in nests of *Rhopalum atlanticum* Bohart (Kislow and Matthews 1977), and as seems to have been the case for some cells in my series.

Although barriers of fill between sets of larval provender do seem to be the rule (Kohl 1915), communal cells, though unusual among crabronids, are known to be a normal attribute of the nests of some species. Thus the nests of *Rhopalum crassinodum* (Spinola) and *R. brevinodum* (Spinola) have no cross-walls, and each nest has but one greatly elongated, communal cell in which 5 or more larvae develop in linear order (Claude-Joseph 1928; generic assignments those of Leclerq 1954). In them, as Krombein holds for *T.* "*amu*" and as is probably so for all *Tracheliodes,* the larvae (at least if fully fed) are neither fatally antagonistic nor cannibalistic. A lack of antagonism, at least in early instars, is most strikingly shown by larvae of *R. claudii* (Herbst) which not only occupy a single communal cell, but hatch from a cluster of 6–10 eggs glued together at the bottom of an otherwise empty, proximally open cell. Once the eggs have hatched, the maternal female progressively provisions the developing larvae with aphid prey (Claude-Joseph 1928). Unless the mother has marked out the walls of the burrow into suitable cell lengths, say, by secretions, and the larvae seek such an individual mark when cocooning, it is difficult to account for the subsequent linear, orderly array of the cocoons of *R. claudii* other than by development of a defensive territorial antagonism on the part of maturing larvae. If there are no wall markings signalling appropriate orientation of the cocoon at that point, it would be expected that cocoons of *R. claudii* would randomly orientate with respect to the burrow's entrance. Regrettably Claude-Joseph does not comment on the orientation of the cocoons.

The cocoons of *T.* "*amu*" and *T. foveolineatus* are closely similar (*cf.* descriptions and figs. 68–69 of Krombein 1967 with my account), they are like those of *T. quinquenotatus* by having the proximal end (facing the open end of the burrow) formed as a flat, tough diaphragm normal to the axis of the burrow, tightly affixed to its walls, and with the distal end evenly rounded. As described and figured by Grandi (1934, 1961, see fig. 131), the constriction of the cocoon of *T. quinquenotatus* is slight and immediately behind the diaphragm, with most of the length

of the cocoon thereafter lying flush with the wall of the burrow. That stands in marked contrast to the relatively narrow body of the cocoon, of both Nearctic species, which is remote from the burrow wall and enclosed in a shroud of ant remains. Ferton's description of the cocoon of *T. quinquenotatus,* however, suggests a closer similarity to the cocoons Krombein and I have described. According to Ferton (1890, 1923), the only contact the cocoon of *T. quinquenotatus* has with the burrow is by the rim of its diaphragm, which has a diameter somewhat greater than the remainder of the cocoon. The latter is free from direct contact with the walls of the burrow, and lies within the encircling remains of ants. The differences between Grandi's and Ferton's accounts clearly reflect only differences in burrow diameters. Such differences in rim to girth dimensions may be expected to be found in cocoons of the Nearctic species from nests of widely different burrow diameter. In principle, a cocoon from a burrow having the smallest acceptable diameter would have a rim at most slightly larger than the least girth of the cocoon, as in Grandi's case.

It is natural to suppose that the flattened disc of the cocoon which faces the open entrance of the burrow marks the *cephalic* end of the cocoon; Grandi, however, has declared that not to be so. Nor is it so for the cocoon of *T. foveolineatus* or, by inference, that of *T. "amu."* The flat disc of the *Tracheliodes* cocoon is the homolog of the caudal end or plate of a typical cocoon of *Crabro* (for which see Enslin 1922) and like that of *Crabro* it receives the larval excrement at the onset of the resting stage, darkening its margins. Unlike a typical cocoon of *Crabro,* which has an apical pore, nipple, and separately spun closure (Hachfeld 1945), the cephalic end is continuous and simply rounded in *Tracheliodes'* cocoon. That the rounded end is in fact the cephalic pole is shown by the orientation of the head ends of the resting larva and *pharate* imago to this pole of the cocoon, and deposition of excrement at the margins of the opposite pole. Oddly, the cocoons of both *T. foveolineatus* and *T. "amu."* thus regularly face the blind end of the burrow with their cephalic ends, the caudal discs of the cocoons simulating anterior walls of cells. Unfortunately, neither Ferton nor Grandi comment on the orientation of the cocoons of *T. quinquenotatus* within their burrow, but very likely they also face the exit tail first.

Once the pupal integument is shed, the slender adult of *T. foveolineatus* reverses its position within the length of the pliant cocoon, rests for several days, and then cuts through the face of the diaphragm or its margin (6 cases), or through the body of the cocoon, behind the diaphragm (2 cases).

It is a mystery as to what the cue or cues may be in the horizontal trap nest to which the spinning larva responds, thereby regularly giving the curious reversal of the usual orientation of a cocoon. Perhaps the wall of the communal cell bears periodic markings of some sort left by the mother toward which the cocoon is compulsively aligned by the larva. Thereafter, when exiting, the wasp appears to respond to the smooth, negative, inner curvature of the cephalic end of its cocoon in the same way that a eumenid larva responds to hind-wall information after the front wall of its cell has been replaced by a flat disc (Cooper 1957). Certainly the facing of cocoons away from the exit is common among crabronid species in which burrows are vertical, or nearly so, with the exit below (see Claude-Joseph 1928, for examples). But here, as with other wasps, response to gravity is sufficient to account for the orientation of the cocoons by spinning larvae.

Summary

The biologic features probably common to species of *Tracheliodes* include development of a linear nest, "rented" or dug, without a closure at the entrance. The nest consists of a single communal cell at most marked into individual larval sectors ("cells") by insubstantial amounts of fill. It is provided with dolichoderine workers as prey, of which some number is stored prior to oviposition. The egg of the wasp is affixed by its cephalic pole adjacent to the procoxal conjunctival membrane of an ant. A rim-fire cartridge-shaped cocoon is spun, with the posterior rim of variable width depending upon the diameter of the burrow. Each cocoon is orientated with the rimmed, disc-like caudal end (and that of its enclosed larva or pupa) facing the entrance of the nest. The soft, pliant body of the cocoon permits reversal and reorientation toward the exit by the enclosed imago within the intact cocoon.

Acknowledgments

I am grateful to my colleague Prof. Jean-Pierre Barricelli for verifying, and then improving, my understanding of Guido Grandi's accounts, to Dr. Karl V. Krombein (of the U.S.N.M.) for painstaking review of my account, and to my wife, Dr. Ruth S. Cooper, for untiring and cheerful help with my fieldwork.

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Taxonomic Notes on Some Delesseriaceae (Rhodophyta) Occurring in Southern California and Mexico

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Type specimens of several taxa in the red algal family Delesseriaceae (Ceramiales), occurring in southern California and/or the Gulf of California, have been examined with particular attention to the anatomy of the apices and the development of the cell rows. On the basis of observations that the lateral pericentral cells do not undergo transverse divisions, that intercalary divisions occur in second-order cell rows, and the fact that bladelets can arise from the midline, *Membranoptera spatulata* Dawson and *Hypoglossum gregarium* Dawson [=*Phrix gregarium* (Dawson) Stewart] are demonstrated to be conspecific and to belong to the genus *Apoglossum*. The new combination *A. gregarium* is made. *Apoglossum punctatum* Dawson is recognized to be a taxonomic synonym of the earlier described *Grinnellia lanceolata* Dawson.

An on-going interest in the systematics of the family Delesseriaceae (Rhodophyta) has led me to examine some of the species described by E. Y. Dawson from the Gulf of California. Dawson's type specimens now reside in the herbaria of three institutions (Silva 1967): the Allan Hancock Foundation, University of Southern California (AHFH); the University of California, Berkeley (UC); and the U.S. National Museum, Washington, D.C. (US), which includes the Beaudette Foundation Herbarium.

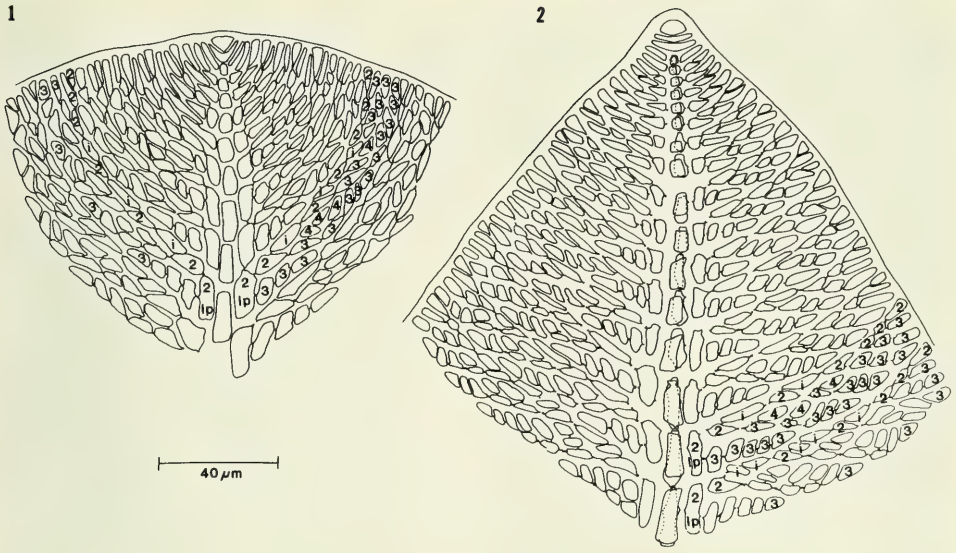
Materials and Methods

The holotype specimens of the following taxa (and the herbaria in which they are deposited) were examined: *Apoglossum punctatum* (US); *Grinnellia lanceolata* (AHFH); *Hypoglossum gregarium* (US); and *Membranoptera spatulata* (AHFH). Figure 13 is based on a collection of *Grinnellia americana* made by R. Wetherbee and D. Checkley (*Wynne 3267* in MICH), 8.vii.1971, Fisheries jetty, Woods Hole, Massachusetts, USA. A Zeiss research microscope fitted with a *camera-lucida* drawing tube and a camera-back was used for this study. The photographs in Figures 3 and 4 were taken with a camera mounted on a Nikon SMZ-10 stereomicroscope.

Results

Hypoglossum gregarium Dawson and Membranoptera spatulata Dawson

Hypoglossum gregarium is an alga that was described from the Gulf of California (Dawson 1966) but later was collected in southern California (Stewart 1974; Stewart and Rüdenberg 1978). This species was the basis of the genus *Phrix* (Stewart 1974). The organization of cell rows in an apical region of the holotype



Figs. 1 and 2. Fig. 1. *Hypoglossum gregarium. Camera lucida* drawing of apex of holotype. Symbols: *2,* cell of 2nd-order row; *3,* cell of 3rd-order row; *4,* cell of 4th-order row; *i,* cell derived from an intercalary division. Fig. 2. *Membranoptera spatulata. Camera lucida* drawing of apex of holotype.

is represented in Fig. 1. Stewart correctly recognized that Dawson's species cannot be placed in *Hypoglossum* because not all tertiary initials reach the thallus margin and cells of second-order rows undergo intercalary divisions. Stewart thus established *Phrix,* distinguishing it from such genera as *Delesseria, Grinnellia,* and *Apoglossum* by the absence of transverse divisions by the lateral pericentral cells in *Phrix.* Additional criteria of her new genus included a conspicuous but unthickened midrib and the vague or indistinct nature of the lateral veins.

Although it is true that the lateral pericentral cells in *Delesseria* and *Grinnellia* undergo transverse divisions, the lateral pericentral cells of *Apoglossum ruscifolium* (Turn.) J. Ag., the type of the genus, have been clearly depicted as not undergoing such transverse divisions (Kylin 1923, 1956; Coppejans 1983; Wynne 1984). The development of the midrib in *A. ruscifolium* is initiated by the cutting off of small cells from the corners of the transverse and lateral pericentral cells (Coppejans 1983, p. 227, fig. 2). These small cells then grow downward, elongating, dividing, and investing the underlying primary cell layer. The lateral pericentral cells, although covered with this rhizoidal cortication, remain undivided transversely (Kylin 1923, fig. 55; Wynne 1984, fig. 28). This difference is a useful feature to distinguish *Apoglossum* from the related genera *Delesseria* and *Grinnellia* (Wynne 1983).

Since *Phrix gregarium* cannot be separated from *Apoglossum* in regard to the behavior of the lateral pericentral cells, one next considers the other criteria employed by Stewart. The poorly developed midrib present in *P. gregarium* is not appreciably different from that of some species of *Apoglossum,* e.g., *A. spathulatum* (Sond.) Womers. and Shepl. and *A. minimum* Yamada. The midrib in specimens of *A. spathulatum,* originating from western Australia (the provenance of the type), was observed to be poorly developed, the onset of rhizoidal cortication

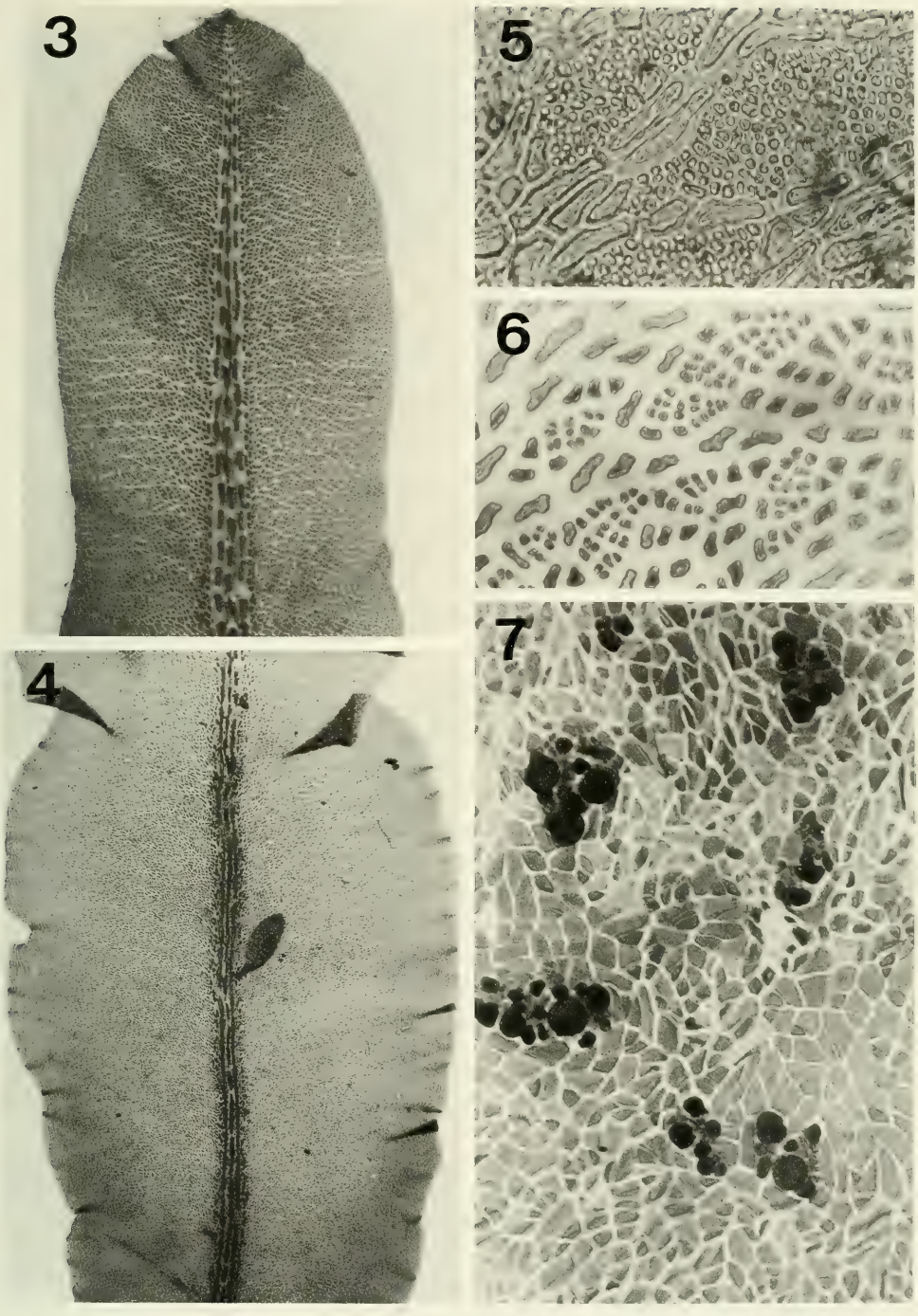
commencing distantly from the apex (Wynne 1984). Stewart's (and my own) examination of the holotype of *Hypoglossum gregarium* revealed that "some cortication does develop in the lower part of the axis, and in stipes" (Stewart 1974). This characteristic of the extent of the development of the midrib accordingly does not prove to be a reliable or significant criterion, especially at the generic level. It is a variable within other genera of the family, such as *Membranoptera* and *Phycodrys.*

Furthermore, Stewart referred to "occasional veins" and "partial veins" caused by the relatively greater elongation of cells in second-order rows, which is essentially the same method by which such lateral veins (or "pellucid striae" referred to by Harvey 1871) are brought about in *Apoglossum.* This appearance may not be dramatically apparent; for example, in *A. minimum* the blades were described as lacking microscopic veins (Yamada 1944). Furthermore, the closely related genus *Delesseria* includes some species with macroscopic veins, some with microscopic veins, and some with no obvious veins (Wynne 1984). The conclusion from these observations is that Dawson's species is assignable to *Apoglossum* and its characteristics do not justify the establishment of a separate genus. The critical evidence includes the fact that lateral pericentral cells do not undergo transverse divisions, intercalary divisions occur in second-order cell rows, and new blades can arise from the midline. A further point of similarity between the Dawson species and *Apoglossum ruscifolium* is the arrangement of the tetrasporangial sori. In *Phrix gregarium* (Stewart 1974) and in *A. ruscifolium* (Kylin 1923; Gayral 1958; Coppejans 1983) there is a pair of linear sori running continuously along either side of the midline of the blade (on both surfaces), and formation of tetrasporangia includes the involvement of the lateral pericentral cells.

Another species, *Membranoptera spatulata,* described also from the Gulf of California by Dawson (1950), was discussed by Stewart (1974) because of the conspicuous midline as was seen in *Phrix gregarium.* Although this similarity was pointed out, Stewart noted that the placement of the former species in *Membranoptera* "seems correct" and that it differed from *P. gregarium* by the regular presence of lateral veins and by the 3rd- and 4th-order cell rows being aligned in "distinctly arranged segments."

The holotype (and only known collection) of *Membranoptera spatulata* was examined. Blades (Fig. 3) have the same unthickened midline, made up of the four conspicuous pericentral cells surrounding the central cell of each segment, as characterized *P. gregarium.* An inspection of the apical region of a blade (Fig. 2) revealed the presence of intercalary divisions in the second-order rows and thus the incorrect assignment of this taxon to *Membranoptera,* in which genus intercalary divisions are lacking (Kylin 1923). The cutting off of new cells in second-order cell rows in a distal manner is characteristic of *Apoglossum* (Kylin 1923; Wynne 1984) as also is the adaxial relationship of 4th-order cell rows to 3rd-order cell rows. The presence, although not common, of bladelets from the midline of parent blades (Fig. 4) is again consistent with *Apoglossum.*

When one next compares these two taxa, both of which conform to *Apoglossum,* one can observe the many points of similarity or identity (Table 1). The wording used in Table 1 is taken directly from the original sources, except where new observations are indicated. The most important points are the conspicuous midline with the lateral pericentral cells not undergoing transverse divisions (Figs. 1



Figs. 3–7. Figs. 3–6. *Membranoptera spatulata.* Holotype collection. Fig. 3. Blade with conspicuous midline. Fig. 4. Formation of a bladelet from the midline of parent blade. Figs. 5 and 6. Spermatangial sori separated by sterile cells. Fig. 7. *Apoglossum punctatum.* Surface view of holotype, showing discrete tetrasporangial sori. Fig. 3, ×112; Fig. 4, ×40; Fig. 5, ×740; Fig. 6, ×728; Fig. 7, ×122.

Table 1. Comparison of features in *M. spatulata* and *H. gregarium.*

	Membranoptera spatulata	*Hypoglossum gregarium*
References	Dawson 1950	Dawson 1966; Stewart 1974
Habit	dense group of blades; tufted	gregarious blades in clumps
Basal system	creeping, spreading	spreading, fleshy
Blade shape	blunt-spatulate	oblanceolate to spatulate
Blade height	10 mm	4–6 mm; 7 mm
Blade width	2.0–2.5 mm	1–2 mm
Lateral nerves	abundant, parallel, regular, microscopic	occasional, partial
Blade margin/surface	margin undulate	surface rippled, undulate
Branching in blades	rarely from midline*	rarely from midline
Lateral pericentral cells	conspicuous; not divided transversely	conspicuous; not divided transversely
Midrib cortication	heavily corticated in lower part of axis and stipe	hyphae in basal region in blade midline and stipe
Intercalary divisions in 2nd-order rows	present*	present
Spermatangial sori	occupying interstices between microscopic veins	patches between the 2nd- and 3rd-order cell rows
Tetrasporangial sori	—	continuous on either side of midline

* New observations from examination of holotype.

and 2), the presence of intercalary divisions in 2nd-order cell rows, and the production of bladelets from the midline (Fig. 4; fig. 4 in Stewart), all of which are diagnostic of *Apoglossum.* It is considered significant that Stewart also observed this production of bladelets from the midline of parent blades in *Phrix.* She regarded such branching as "possibly related to damage or infection." My interpretation is that such branching is perfectly normal, although infrequent, for this species and is in full agreement with *Apoglossum.*

The many other features of habit, dimensions, and the restriction of rhizoidal cortication to the proximal part of the midline of blades and the stipes are evidence for the conspecificity of these two taxa. Perhaps most persuasive is the nature of the spermatangial sori. It is fortunate that male plants are known for both taxa, and they are identical: small, elongate sori in patches among the sterile cells of 2nd- and 3rd-order cell rows (Figs. 5 and 6; fig. 9 in Stewart). This arrangement is different from that of *A. ruscifolium,* in which the male sori form a series of narrow bands running diagonally from the midrib toward the blade margins (Kylin 1923).

The apparent point of disagreement has to do with the lateral nerves, which were reported to be abundant and regular in *M. spatulata* (Dawson 1950) but occasional or partial in *H. gregarium* (Stewart 1974). The very fact that lateral veins *are* detectable in *H. gregarium* is the most telling fact, namely, that it conforms to *Apoglossum.* Indeed Stewart (1974) stated that veins were "not a consistently useful diagnostic character." I would account for this apparent disagreement as simply a matter of variation present in populations of a single species. I cannot concur with Stewart's contention that simply because of intercalary divisions in secondary and higher orders of cell rows, these rows cannot be traced clearly away from the apex. Figures 1 and 2 provide a sufficient amount of on-

togenetic information on blade development to permit recognition of the essentially identical pattern present in the two holotypes.

The conclusion from the foregoing discussion is that we are dealing with a single species of *Apoglossum* occurring in the Gulf of California and southern California. Of these species discussed, *Membranoptera spatulata* is the older. The combination of *A. spatulata,* however, is pre-empted by *A. spathulata* (Sond.) Womers. and Shepl. (1982), and *spathulata* and *spatulata* are sufficiently similar to be confused. *Hypoglossum gregarium* then is available, and the following combination is made:

Apoglossum gregarium (Dawson) comb. nov.

Basionym: *Hypoglossum gregarium* Dawson, 1966, J. Ariz. Acad. Sc. 4, p. 65, fig. 6C.

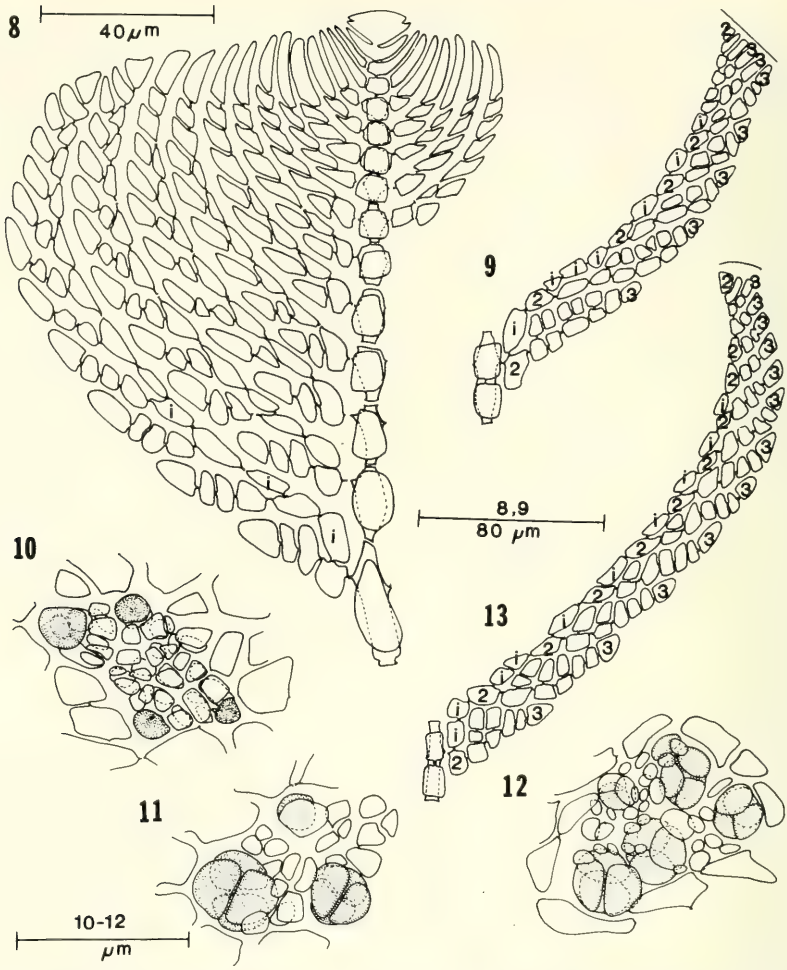
Synonym: *Membranoptera spatulata* Dawson, 1950, p. 157, fig. 15. *Phrix gregarium* (Dawson) Stewart, 1974, p. 147.

Apoglossum gregarium bears some resemblance to *A. minimum* Yamada (1944), a species which has never been illustrated and is known only from the type specimen and two other collections (Dr. M. Chihara, pers. comm.). *Apoglossum gregarium* differs from that species by the development of branches gregariously from a spreading, fleshy basal disc rather than by producing lateral blades from the erect blades as seen in the Japanese species. Blades of *A. minimum* are attached by an irregularly shaped, discoid base.

Apoglossum punctatum Dawson and Grinnellia lanceolata Dawson

Apoglossum punctatum was described (Dawson, 1966) on the basis of a single tetrasporic specimen which measured 26 mm in height and was illustrated by a figure of the habit, showing the small punctate sori said to be distinctive of the species. The apical region of the holotype of *A. punctatum* has been examined and is presented in Figure 8. Figure 9 illustrates the products of division of a second-order cell row from a single lateral pericentral cell at a distance of 17 segments from the apical cell. What is readily apparent by these figures of the ontogenetic development of the blade is that this taxon does not conform to *Apoglossum,* a genus in which the lateral pericentral cells do not undergo transverse divisions (Kylin 1923).

The pattern exhibited by the apex and the scattered, very small tetrasporangial sori (Figs. 7, 10–12) is in full agreement with these characteristics in *Grinnellia.* The type of *Grinnellia, G. americana* (C. Ag.) Harv., has a distribution in the western North Atlantic and the Gulf of Mexico (Taylor 1942, 1960; Dawes 1974; Kapraun 1980). The apical region of a blade of *G. americana* was examined and observed to show the same ontogenetic development as present in the type of *A. punctatum.* A representative view of a second-order cell row and its products is seen in Figure 13 at a comparable distance from the apex as in Figure 9. A second species, *G. lanceolata* Dawson (1944), occurring in the Gulf of California, was originally described as having a height of 2.5 cm, almost the exact height for *A. punctatum.* Subsequently, Dawson (1962) stated the height to range from 2.5 to 6.0 cm for *G. lanceolata.* The evidence indicates that Dawson's *A. punctatum* belongs to *Grinnellia* and that it is indistinguishable from Dawson's own *G. lanceolata,* which is known also in sublittoral habitats from the Gulf of California.



Figs. 8–13. Figs. 8–12. *Apoglossum punctatum.* Fig. 8. *Camera lucida* drawing of apex of holotype. *i,* cell derived from an intercalary division. Fig. 9. Cell rows produced from a single lateral pericentral cell located 17 segments from an apical cell. *2,* cell of 2nd-order cell row; *3,* initial of 3rd-order row. Figs. 10–12. Tetrasporangial sori. Fig. 13. *Grinnellia americana.* Cell rows produced from a single lateral pericentral cell, located 17 segments from an apical cell.

Acknowledgments

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Seasonal Spawning Cycle of Merluza, *Merluccius gayi* (Merluccidae) from Chile

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The merluza, *Merluccius gayi* is one of the important marine resources of Chile. Yearly landings during 1970–79 averaged 45,574 tons a year (Corporación de Fomento de la Producción 1980). The fish's range extends from Antofagasta (23°38′S) to Chiloe (43°00′S) (Corporación de Fomento de la Producción 1980). Except for the study of Balbontín and Fischer (1981) little information exists on reproduction in this species. This report contains the first histological analysis of the *M. gayi* spawning cycle.

A total of 114 specimens were collected from Valparaiso Bay (33°00′S, 71°38′W), Región de Valparaíso, Chile during August 1981–January 1982 and March 1982–August 1982. Collections were made during one day around the middle of each month (day 10–15) between 0500–0700. Fish weights and fresh ovary weights were taken to the nearest g. Fish lengths were measured to the nearest cm. Ovaries were preserved in 10% formalin. Gonosomatic indices (GSI = ovary weight/fish weight × 100) were calculated. Histological sections were cut at 8 μm and stained with Harris' hematoxylin followed by eosin counterstain. Fish averaged 672.9 g weight and 46.3 cm total length.

I used the occurrence of hydrated eggs to identify fish in which spawning was

Table 1. Monthly distribution of body sizes (total lengths) and stages in *Merluccius gayi* spawning cycle, August 1981–1982

Month	N	Range (cm)	Regressed (%)	Previtel-logenic (%)	Vitel-logenic (%)	Mature follicles (no hydrated eggs or postovu-latory follicles) (%)	Hydrated eggs (%)	Post-ovulatory follicles (%)
Aug.	8	43–52	0	0	0	37	37	26
Sept.	9	39–48	33	0	11	11	11	33
Oct.	8	38–52	0	25	0	63	12	0
Nov.	14	39–56	0	0	0	43	43	14
Dec.	8	39–45	25	25	0	38	12	0
Jan.	9	42–69	0	0	12	44	44	0
Mar.	9	36–54	0	0	0	22	67	11
Apr.	10	39–49	0	0	0	50	50	0
May	11	41–54	0	0	0	27	73	0
Jun.	10	44–60	0	0	0	90	0	10
Jul.	8	43–54	0	0	0	25	63	12
Aug.	10	47–59	0	0	0	20	50	30

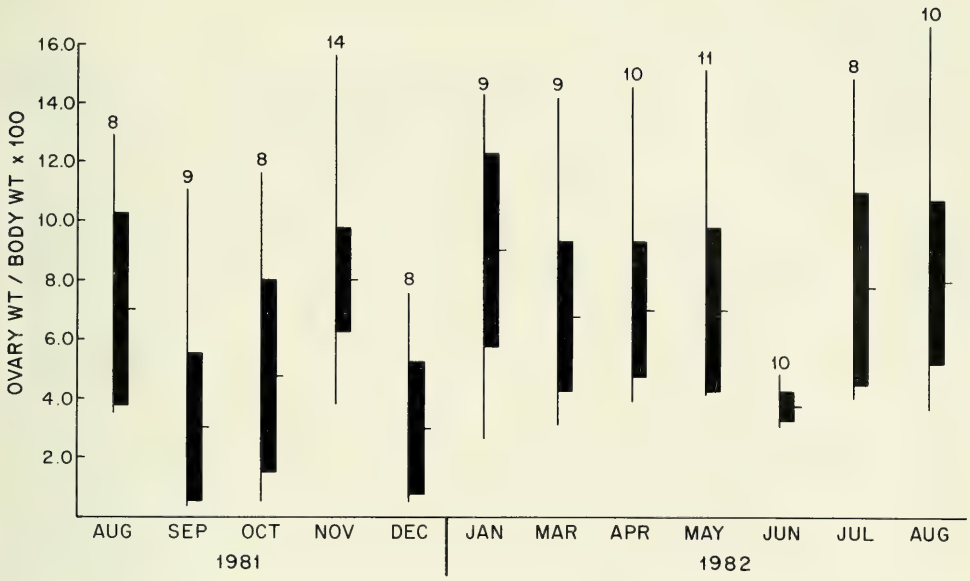

Fig. 1. Seasonal gonosomatic indices for *Merluccius gayi*. Vertical line = range; horizontal line = mean; rectangle = 95% confidence interval. Sample size above each month.

imminent. During hydration, the oocyte grows to as much as four times its original volume (Wallace and Selman 1981) making these structures readily identifiable. Also, I used the presence of postovulatory follicles as proof of a recent spawning. These structures are remnants of the granulosa layer of the spawned egg which hypertrophy and form the convoluted postovulatory follicle. It was determined by Hunter and Goldberg (1980) that the postovulatory follicle has a brief existence in the northern anchovy, *Engraulis mordax* and is indistinguishable from atretic follicles after 48 hours.

The presence of ovaries with postovulatory follicles (evidence of recent spawning) alongside mature eggs (489 μm diameter) (upcoming spawning) and vitellogenic eggs (252 μm diameter) with yolk deposition in progress for a future spawning indicate *M. gayi* is a multiple spawning fish. Representatives of the *M. gayi* population were reproductively active in all months investigated (Table 1). Seasonal gonosomatic indices (Fig. 1) showed no discernible seasonal gonadal cycle. Females with regressed (inactive) ovaries which contained primary oocytes (74 μm) were common only in September and December (Table 1). During October and December slightly enlarged previtellogenic oocytes (137 μm) appeared. These oocytes contain a ring of vacuoles around their inner periphery. Nevertheless, spawning activity was clearly in progress during these months. Females with postovulatory follicles were found in 58% of months examined and females with hydrated eggs in 97% of months examined. The smallest reproductively active female measured 36.5 cm (total length) and was in spawning condition.

The spawning cycle of *M. gayi* differs from that of other hake. Christiansen and Cousseau (1971) found *Merluccius merluccius hubbsi* off Argentina to have two spawning periods, a main one in summer (October–March) and another one in winter (June–July). In contrast, MacGregor (1966) reported the Pacific hake,

Merluccius productus, spawns once a year with over 98% of the spawning between January–April (MacGregor 1971).

Balbontín and Fischer (1981) reported that *M. gayi* from Chile spawn throughout the year. They found the greatest number (ca. 30%) of sexually ripe females from August–November. My data indicated no such seasonal pattern in distribution of ripe females. This could be due to my small sample sizes.

Foucher and Beamish (1980) found that *M. productus* spawning occurs in April or May in the Strait of Georgia, Canada (49°N, 123°W). Smaller residual yolked oocytes are resorbed in this population after the largest yolked oocytes become hydrated so that a second spawning does not occur. This appears to be a basically different system than that which occurs in the *M. gayi* population described herein. No traces of this post-spawning resorption of oocytes were observed in my samples although a few females were found in a regressed state in September and December and a few in a previtellogenic state in November and December.

In conclusion, on the basis of the occurrence of hydrated eggs (spawning imminent) or postovulatory follicles (recent spawning), my data show *M. gayi* spawning occurs throughout the year at Valparaiso, Chile. Moreover, the presence in the same ovary of postovulatory follicles (recent spawning) alongside mature follicles (subsequent spawning) indicate *M. gayi* is a multiple spawning fish.

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INDEX TO VOLUME 84

Aguilar, Alvaro Tresierra, see Stephen R. Goldberg
Allen, Larry G.: A Habitat Analysis of the Nearshore Marine Fishes from Southern California, 133
Asymmetriode ambodistorta, n. sp., 104

Blake, James A., see Jerry D. Kudenov
Blankenship, Daniel J. and Gary L. Bradley: Electrophoretic Comparison of Two Southern California Chipmunks (*Tamias obscurus* and *Tamias merriami*), 48
Bleich, Vernon C., see Orlando A. Schwartz
Bradley, Gary, see Daniel J. Blankenship

Cooper, Kenneth W.: Flight Period, Range Extension, and Variability of *Heteranthidium autumnale* Snelling (Hymenoptera: Megachilidae), 53
Cooper, Kenneth E.: The Nest of *Tracheliodes foveolineatus* (Viereck), and Normal Reversal of Cocoon Orientation Within it (Hymenoptera: Sphecidae: Crabroninae), 156
Crabtree, C. Ben: Sexual Dimorphism of the Upper Jaw in *Gillichthys mirabilis,* 96

Durham, Floyd E., see William F. Samaras

Egoscue, Harold J.: Kit Fox Flea Relationships on the Naval Petroleum Reserves, Kern County, California, 127

Garthwaite, Ronald L., F. G. Hochberg, and C. Sassaman: The Occurrence and Distribution of Terrestrial Isopods (Oniscoidea) on Santa Cruz Island with Preliminary Data for the Other California Islands, 23
Goldberg, Stephen R.: Seasonal Spawning Cycle of Merluza, *Merluccius gayi* (Merluccidae) from Chile, 172
Goldberg, Stephen R. and Alvaro Tresierra Aguilar: Notes on Spawning in the Dolphin Fish, *Coryphaenia hippurus* (Coryphaenidae) from Peru, 51

Hochberg, F. G., see Ronald L. Garthwaite

Kudenov, Jerry D. and James A. Blake: A New Species of *Pseudeurythoe* (Polychaeta: Amphinomidae) from Central California, 38

Lavoie, Derrick R.: Population Dynamics and Ecology of Beach Wrack Macroinvertebrates of the Central California Coast, 1
Lea, Robert N. and Marija Vojkovich: Record of the Pacific Burrfish from Southern California, 46
Lindberg, David R.: Crab Predation on Intertidal Populations of the Urchin *Strongylocentrotus purpuratus,* 109

Markham, John C.: A New Species of *Asymmetrione* (Isopoda: Bopyridae) Infesting the Hermit Crab *Isocheles pilosus* (Holmes) in Southern California, 104

Pseudeurythoe reducta, n. sp., 39

Reynolds, Richard L.: Domestic Dog Associated with Human Remains at Rancho La Brea, 76

Samaras, William F. and Floyd E. Durham: Feeding Relationships of Two Species of Epizoic Amphipods and the Gray Whale, *Eschrichtium robustus,* 113

Sassaman, C., see Ronald L. Garthwaite

Schwartz, Orlando A. and Vernon C. Bleich: Optimal Foraging in Barn Owls? Rodent Frequencies in Diet and Fauna, 41

Shermis, Stewart: Canine Fracture Avulsion in *Smilodon californicus,* 86

Soule, Dorothy F., see John D. Soule

Soule, John D. and Dorothy F. Soule: Bryozoa from Seagrass Beds of the Northern Saudi Arabian Coast: Distribution and Seasonality, 67

Vojkovich, Marija, see Robert N. Lea

Wilson, Edward C.: The Spiral Trace Fossil *Gyrolithes* de Saporta, 1884 in the Pliocene Tirabuzon Formation Near Santa Rosalia, Baja California Sur, Mexico, 57

Wynne, Michael J.: Taxonomic Notes on Some Delesseriaceae (Rhodophyta) Occurring in Southern California and Mexico, 164

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CONTENTS

Feeding Relationship of Two Species of Epizoic Amphipods and the Gray Whale, *Eschrichtius robustus*. By *William F. Samaras and Floyd E. Durham* 113

Kit Fox Flea Relationships on the Naval Petroleum Reserves, Kern County, California. By *Harold J. Egoscue* 127

A Habitat Analysis of the Nearshore Marine Fishes from Southern California. By *Larry G. Allen* 133

The Nest of *Tracheliodes foveolineatus* (Viereck), and Normal Reversal of Cocoon Orientation Within it (Hymenoptera: Sphecidae: Crabroninae). By *Kenneth W. Cooper* 156

Taxonomic Notes on Some Delesseriaceae (Rhodophyta) Occurring in Southern California and Mexico. By *Michael J. Wynne* 164

Seasonal Spawning Cycle of Merluza, *Merluccius gayi* (Merluccidae) from Chile. By *Stephen R. Goldberg* 172

Index 175

COVER: Mature gray whale barnacle (*Cryptolepas rhacianecti*) and encrusting whale lice (*Cyamus scammoni*). Photo by William F. Samaras and Floyd E. Durham.